

Review

The Importance of Microorganisms for Sustainable Agriculture—A Review

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Abstract: In the face of climate change, progressive degradation of the environment, including agricultural land negatively affecting plant growth and development, endangers plant productivity. Seeking efficient and sustainable agricultural techniques to replace agricultural chemicals is one of the most important challenges nowadays. The use of plant growth-promoting microorganisms is among the most promising approaches; however, molecular mechanisms underneath plant–microbe interactions are still poorly understood. In this review, we summarized the knowledge on plant–microbe interactions, highlighting the role of microbial and plant proteins and metabolites in the formation of symbiotic relationships. This review covers rhizosphere and phyllosphere microbiomes, the role of root exudates in plant–microorganism interactions, the functioning of the plant’s immune system during the plant–microorganism interactions. We also emphasized the possible role of the stringent response and the evolutionarily conserved mechanism during the established interaction between plants and microorganisms. As a case study, we discussed fungi belonging to the genus *Trichoderma*. Our review aims to summarize the existing knowledge about plant–microorganism interactions and to highlight molecular pathways that need further investigation.

Keywords: microbiome; PGPM; plant fitness; bioinoculants; symbiotic interactions; *Trichoderma*; stringent response; *RSH* genes; rhizosphere; alarmones



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1. Introduction

Traditional agricultural techniques, such as chemical fertilizers, pesticides, fungicides, and herbicides, enable the protection of crop plants against pathogens and ensure better yield. Chemical compounds present in agricultural chemicals are harmful to the environment and cause soil, atmosphere, and water pollution [1]. These compounds are the reason for the extinction of fish [2], bees [3], and plants [4,5], and pose a threat to the biodiversity of soil bacterial [6–8] and fungal communities [9]. Chemical plant protection products negatively affect agricultural soils, i.e., they change soil physical properties, (e.g., texture, permeability, porosity), they disturb the cycle of the elements, such as phosphorus and nitrogen, and they decrease the complexity of soil microbiome [10]. In the face of a growing world population and increased demand for food both in terms of food quantity and food quality, the usage of bioinoculants, i.e., biofertilizers to increase the yield and biopesticides to protect plants, is the future of agriculture. Bioinoculants comprised of living or dormant microbes that are able to promote plant growth and development are called PGPM (plant growth-promoting microorganisms) and have great potential not only for enhancing plant yield but also for remediation of degraded soils [11–13]. Bioinoculants are cost-effective and environmental-friendly approaches in agriculture [14]. The first step in a bioinoculant formulation is the isolation and identification of a microbe. The further potential of a particular microorganism for plant growth promotion needs to be verified, and this ability should be confirmed in laboratory and field conditions. Moreover, potential risks to other organisms, such as animals and natural soil microbiomes, should be also determined [15]. The

best-known examples of PGPM are mycorrhizal fungi and bacteria belonging to *Rhizobium*; however, plant growth-promoting microorganisms are found among varied taxa of bacteria, fungi, and algae [16]. In Table 1, several examples of PGPM are shown.

Table 1. Examples of plant growth-promoting microorganisms. The effect of PGPM on plants and, if known, the mode of action of microorganisms is also included.

PGPM	Plant	Remarks	References
		Bacteria	
<i>Acinetobacter</i> sp. RG30, <i>Pseudomonas putida</i> GN04	<i>Zea mays</i>	Plant: - increased tolerance to Cu - enhanced chlorophyll content - increased Cu concentration in tissues Bacteria: - IAA synthesis - production of siderophores - solubilization of Cu and P	[17]
<i>Acinetobacter</i> sp. RSC9	<i>Saccharum</i> sp.	Plant: - under salt stress enhanced number of leaves, fresh, dry weight, and germination ratio Bacteria: - IAA production - P, K, and Zn solubilization - N ₂ assimilation	[18]
<i>Agrobacterium</i> sp. 10C2	<i>Phaseolus vulgaris</i>	- increased nodule formation - higher plant biomass - enhanced content of P, polyphenols, and flavonoids in grains - changes in the structure of the microbial community	[19]
<i>Arthrobacter globiformis</i>	<i>Zea mays</i> , <i>Triticum aestivum</i>	Plant: - enhanced biomass, uptake of Fe and P, and higher chlorophyll content under iron-stress Bacteria: - siderophores production	[20]
<i>Arthrobacter</i> sp., <i>Bacillus megaterium</i>	<i>Lycopersicon esculentum</i>	- enhanced seed germination ratio, seedling length, and dry and fresh weight under salt stress	[21]
<i>Azospirillum brasilense</i>	<i>Cicer arietinum</i>	- increased resistance to <i>Ascochyta rabiei</i> via induction of plant defense-related genes (<i>Snakin2</i> and <i>DEF0422</i>)	[22]
<i>Azospirillum lipoferum</i>	<i>Triticum aestivum</i>	- improved germination, plant growth, higher chlorophyll content, and improved membrane stability under salt stress - increased production of SOD and osmolytes, i.e., proline, soluble protein, and sugars under salt stress	[23]
<i>Azotobacter</i> spp.	<i>Zea mays</i>	Plant: - increased shoot dry weight, chlorophyll content, and N, P, Fe concentration under drought stress Bacteria: - production of siderophores	[24]
<i>Bacillus amyloliquefaciens</i>	<i>Zea mays</i>	- increased tolerance to salt stress, enhanced content of chlorophyll, soluble sugars, and glutathione, higher peroxidase/catalase activity	[25]

Table 1. Cont.

PGPM	Plant	Remarks	References
<i>Bradyrhizobium</i> sp., <i>Rhizobium leguminosarum</i> , <i>Azotobacter</i> sp.	<i>Gossypium hirsutum</i>	Plant: - increased rate of seedling emergence, biomass, and N uptake Bacteria: - IAA production	[26]
<i>Burkholderia phytofirmans</i> PsJN	<i>Triticum aestivum</i>	- improved water content and CO ₂ assimilation rate, water use efficiency, chlorophyll content, and higher yield under drought stress - improved ionic balance, antioxidant levels, higher N, P, K, and protein content in grains	[27]
<i>Burkholderia tropica</i>	<i>Lycopersicum esculentum</i>	Plant: - increased yield Bacteria: - N-fixation and P solubilization	[28]
<i>Enterobacter cloacae</i>	<i>Spinacia oleracea</i>	- protection against <i>Fusarium</i> wilt (<i>Fusarium oxysporum</i>)	[29]
<i>Frankia</i> spp.	<i>Casuarina glauca</i> , <i>Casuarina equisetifolia</i>	- salt stress alleviation, higher dry biomass, chlorophyll, and proline content	[30]
<i>Methylobacterium</i> sp. 2A	<i>Arabidopsis thaliana</i> , <i>Solanum tuberosum</i>	Plant: - the alleviation of salt stress of <i>A. thaliana</i> , with higher lateral roots density, number of leaves, and larger rosette diameter - reduced necrotic lesions and chlorosis in <i>S. tuberosum</i> infected with <i>P. infestans</i> Bacteria: - production of IAA, P solubilization, biocontrol activity against <i>Phytophthora infestans</i> , <i>Botrytis cinerea</i> , and <i>Fusarium graminearum</i>	[31]
<i>Pseudomonas putida</i>	<i>Lycopersicum esculentum</i>	Plant: - increased plant height, stem diameter, radical volume, dry biomass, and fruit yield Bacteria: - production of IAA	[32]
<i>Pseudomonas</i> sp. DW1	<i>Solanum melongena</i>	- salt stress ameliorating effect, with increased dry weight, and seed germination - higher SOD activity in leaves	[33]
<i>Pseudomonas stutzeri</i> ISE12	<i>Brassica napus</i>	- enhanced growth under salt stress, with a decrease in non-enzymatic antioxidants accumulation - improved seed germination ratio, number of leaves, chlorophyll content, and dry weight	[34]
<i>Rhizobium leguminosarum</i> , <i>Rhizobium</i> sp., <i>Bradyrhizobium</i> sp.	<i>Oryza sativa</i>	Plant: - increased yield and uptake of N, P, K, and Fe - improved seed vigor, dry biomass, and leaf area with faster seedling emergence Bacteria: - production of IAA	[35,36]
<i>Serratia marcescens</i>	<i>Solanum melongena</i>	- salt stress alleviation, decreased Na ⁺ /Cl ⁻ content in leaves, lower lipid peroxidation level, and higher activity of antioxidant enzymes - enhanced biomass, longer stems, and bigger leaf area	[37]

Table 1. Cont.

PGPM	Plant	Remarks	References
<i>Serratia proteamaculans</i> , <i>Pseudomonas putida</i> , <i>Pseudomonas aeruginosa</i>	<i>Triticum aestivum</i>	Plant: - salt stress alleviation with enhanced plant height, root length, and yield, and higher chlorophyll content Bacteria: - ACC deaminase production	[23]
<i>Streptomyces</i> sp.	<i>Arabidopsis thaliana</i> , <i>Lycopersicon esculentum</i>	Plant: - salt stress alleviation with increased biomass, chlorophyll content, and decreased proline content Bacteria: - production of IAA, ACC deaminase, P, and NaCl solubilization	[38]
<i>Streptomyces</i> sp.	<i>Medicago sativa</i>	- protection against root-lesion nematode (<i>Pratylenchus penetrans</i>)	[39]
Fungi			
<i>Alternaria solani</i> IA300	<i>Capsicum annum</i>	- enhanced number of leaves, flowers, dry, and fresh weight	[40]
<i>Apergillus niger</i> 9-p	<i>Phaseolus vulgaris</i>	Plant: - increased biomass Fungus: - production of IAA, ACC deaminase, siderophores, protease, amylase, pectinase, xylanase, and P solubilization	[41]
<i>Aspergillus fumigatus</i>	<i>Glycine max</i>	Plant: - salt stress alleviation with enhanced biomass, leaf area, chlorophyll content, and photosynthetic rate - increased isoflavones, proline, SA, and JA content and lower ABA content Fungus: - GAs production (GA4, GA9, GA12)	[42]
<i>Collybia tuberosa</i> , <i>Clitocybe</i> sp., <i>Laccaria laccata</i> , <i>Hebeloma mesophaeum</i> , <i>Cyathus olla</i>	<i>Brassica napus</i>	Plant: - enhanced root and shoot growth, number of leaves, and biomass Fungi: - production of IAA	[43]
<i>Funneliformis mosseae</i> , <i>Ensifer meliloti</i>	<i>Vitis vinifera</i>	- enhanced plant height and dry weight - higher VOCs content in roots	[44]
<i>Fusarium equiseti</i> , <i>Glomus mosseae</i>	<i>Cucumis sativus</i>	- protection against anthracnose (<i>Colletotrichum orbiculare</i>) and damping off (<i>Rhizoctonia solani</i>) - enhanced shoot dry weight	[45]
<i>Fusarium verticillioides</i> , <i>Humicola</i> sp.	<i>Glycine max</i>	- salt stress alleviation with increased shoot length, protein content, carotenoid, salicylic acid (SA), and enhanced SOD activity - decreased ABA level and lipid peroxidation level	[46]
<i>Glomus intraradices</i> , <i>Glomus mosseae</i>	<i>Olea europaea</i>	- enhanced yield, dry weight, height, stem diameter, and root length	[47]

Table 1. Cont.

PGPM	Plant	Remarks	References
<i>Lecanicillium psalliotae</i>	<i>Elettaria cardamomum</i>	Plant: - enhanced shoot and root length, biomass, and number of leaves - higher chlorophyll content Fungus: - production of IAA, ammonia, siderophores, and cell-wall degrading enzymes - P and Zn solubilization	[48]
<i>Mortierella antarctica</i> , <i>Mortierella. Verticillata</i>	<i>Triticum aestivum</i>	Plant: - enhanced fresh weight Fungi: - production of IAA, GA, and ACC deaminase	[49]
<i>Mucor sp.</i>	<i>Arabidopsis arenosa</i>	- heavy metal (Zn, Cd, Fe, Pb) stress alleviation with enhanced biomass, root hair growth, improved water, and P content - upregulation of genes involved in nutrient acquisition (<i>HRS1</i> , <i>SPX1</i> , <i>MGD2</i>), and metal homeostasis (<i>MTPA2</i> , <i>ZIP7</i> , <i>IREG2</i> , <i>IRT2</i>)	[50]
<i>Penicillium bilaai</i>	<i>Pisum sativum</i>	- increased root dry weight, length, and P content in the shoot	[51]
<i>Penicillium sp.</i> , <i>Penicillium radicum</i> , <i>Penicillium bilaiae</i>	<i>Medicago lupulina</i> , <i>Lens culinaris</i> , <i>Triticum aestivum</i>	- enhanced shoot growth and dry weight, and increased P uptake	[52]
<i>Phoma sp.</i>	<i>Cucumis sativus</i> , <i>Arabidopsis thaliana</i>	- protection against cucumber mosaic virus (CMV) via ISR - higher number of leaves, increased fresh/dry weight, and the yield of cucumber	[53]
<i>Phoma spp.</i> , <i>Trichoderma asperellum</i> , <i>Fusarium equiseti</i> , <i>Penicillium simplicissimum</i>	<i>Allium cepa</i>	- protection against white rot disease (<i>Sclerotium cepivorum</i>) with enhanced plant height, dry weight, and bulb perimeter - enhanced levels of peroxidase and polyphenol oxidase - upregulation of plant defense genes (<i>PR1</i> , <i>PR2</i>)	[54]
<i>Purpureocillium lilacinum</i> , <i>Purpureocillium lavendulum</i> , <i>Metarhizium marquandii</i>	<i>Zea mays</i> , <i>Phaseolus vulgaris</i> , <i>Glycine max</i>	Plant: - enhanced plant height and biomass and N content in roots (<i>Z. mays</i>) and P in shoots (<i>P. vulgaris</i>) Fungi: - P solubilization and IAA production	[55]
<i>Trichoderma hamatum</i> , <i>Trichoderma harzianum</i> , <i>Trichoderma viride</i>	<i>Freesia refracta</i>	- accelerated flowering and enhanced development of lateral inflorescence shoots - increased K, Fe, Mn, and Zn uptake	[56]
<i>Trichoderma harzianum</i>	<i>Curcuma longa</i>	Plant: - enhanced plant height and yield Fungi: - biocontrol activity against rhizome rot and leaf blight (<i>Pythium aphanidermatum</i> , <i>Rhizoctonia solani</i>) - production of IAA, HCN, cellulase, and P solubilization	[57]
<i>Trichoderma phayaoense</i>	<i>Cucumis melo</i>	Plant: - enhanced plant development, biomass, and fruit yield Fungus: - biocontrol activity against gummy stem blight pathogens (<i>Stagonosporopsis cucurbitacearum</i> , <i>Fusarium equiseti</i>)	[58]
<i>Trichoderma viride</i>	<i>Brassica napus</i>	- enhanced biomass, lateral roots development, and germination ratio - changes in microbial composition	[59]

Table 1. Cont.

PGPM	Plant	Remarks	References
		Algae	
<i>Anabaena oryzae</i> , <i>Anabaena doliolum</i> , <i>Phormidium fragile</i> , <i>Calothrix geitonos</i> , <i>Hapalosiphon intricatus</i> , <i>Aulosira ferilissima</i> , <i>Tolypothrix tenuis</i> , <i>Oscillatoria acuta</i> , <i>Plectonema boryanum</i>	<i>Oryza sativa</i>	- enhanced shoot and root length and biomass - improved protein, phenolics, flavonoids, and chlorophyll content - a higher activity of enzymes (peroxidase, phenylalanine, and ammonia lyase) - elevated levels of IAA, and IBA	[60]
<i>Anabaena variabilis</i> , <i>Anabaena laxa</i>	<i>Lycopersicon esculentum</i>	- protection against Fusarium wilt (<i>F. oxysporum</i>) with significant enhancement of growth, yield, and fruit quality - increased N, P, and Zn concentration - increased activity of defense enzymes (phenylalanine ammonia-lyase, polyphenol oxidase), increased activity of chitosanase, and β -1,3-glucanase	[61]
<i>Calothrix elenkinii</i>	<i>Oryza sativa</i>	- enhanced root/shoot length and fresh weight - improved chlorophyll and IAA content - higher nitrogenase and CMCCase activity - 10-fold increase in microbiome population abundance	[62]
<i>Calothrix sp.</i> , <i>A. laxa</i> , <i>Anabaena torulosa</i> , <i>Anabaena azollae</i> , <i>Anabaena oscillarioides</i>	<i>Triticum aestivum</i>	- enhanced biomass - nitrogen-fixing potential - higher endoglucanase activity	[63]
<i>Chlorella fusca</i>	<i>Cucumis sativus</i>	- protection against anthracnose (<i>Colletotrichum orbiculare</i>) via the induction of SAR	[64]
<i>Chlorella oocystoides</i> , <i>Chlorella minutissima</i>	<i>Zea mays</i>	- enhanced chlorophyll, P, and K content - improved biomass	[65]
<i>Chlorella vulgaris</i>	<i>Telfairia occidentalis</i>	- enhanced germination ratio - higher number of leaves and yield - improved chlorophyll, carbohydrates, proteins, and lipid content	[66]
<i>Microcystis aeruginosa</i>	<i>Oryza sativa</i>	- heavy metal (Cd) stress alleviation with decreased Cd accumulation, increased translocation of Cd from root to shoot, and enhanced dry weight	[67]
<i>Nostoc sp.</i>	<i>Triticum aestivum</i> , <i>Oryza sativa</i>	Plant: - enhanced biomass and shoot/root length Algae: - production of IAA and zeatin	[68]
<i>Nostoc sp.</i>	<i>Zea mays</i>	- enhanced dry mass - higher N content - production of exopolysaccharide	[69]
<i>Scenedesmus quadricauda</i> , <i>Chlorella vulgaris</i>	<i>Lycopersicon esculentum</i>	- enhanced biomass and root length	[70]
<i>Spirulina platensis</i>	<i>Zea mays</i>	- cadmium stress alleviation with improved photosynthetic electron flows and increased non-photochemical quenching - enhanced seed germination, shoot length, root fresh weight, and bigger leaf area - decreased Cd accumulation in shoot	[71]

Table 1. Cont.

PGPM	Plant	Remarks	References
Mixed inoculants			
<i>Anabaena</i> ssp., <i>Calothrix</i> sp., <i>Providencia</i> sp.	<i>Triticum aestivum</i>	- enhanced yield and Fe, Cu, Zn, Mn, and protein content of grains	[72]
<i>Glomus fasciculatum</i> , <i>Bacillus subtilis</i>	<i>Tagetes erecta</i>	- enhanced flowering, with improved fresh weight and color of flowers	[73]
<i>Klebsiella variicola</i> , <i>Glomus multisubtensum</i> , <i>Rhizophagus intraradices</i>	<i>Helianthus tuberosus</i>	Plant: - enhanced biomass, yield, plant height, and leaf area - increased content of inulin in tubers Microbes: - P solubilization and IAA production	[74]
<i>Mesorhizobium mediterraneum</i> , <i>Rhizophagus irregulari</i>	<i>Cicer arietinum</i>	- enhanced yield and protein content of grain under water deficit conditions	[75]
<i>Rhizophagus intraradices</i> , <i>Glomus aggregatum</i> , <i>Glomus viscosum</i> , <i>Claroideoglomus etunicatum</i> , <i>Claroideoglomus claroideum</i> , <i>Pseudomonas fluorescens</i> , <i>Linum usitatissimum</i>	<i>Solanum lycopersicum</i>	- enhanced flower and fruit production, with increased lycopene, vitamins, sugars, and citric acid content of the fruits	[76]
<i>Rhizophagus intraradices</i> , <i>Pseudomonas</i> sp., <i>Bacillus</i> sp.	<i>Sulla carnosa</i>	Plant: - enhanced biomass, stomatal conductance, photosynthetic pigment content, and photosynthesis rate under salt stress - increased proline content and higher activity of antioxidative enzymes Microbes: - production of IAA	[77]
<i>Septoglomus constrictum</i> , <i>Diversispora aumantia</i> , <i>Archaeospora trapei</i> , <i>Glomus versiforme</i> , <i>Paraglomus oculatum</i> , <i>Bacillus thuringiensis</i>	<i>Lavandula dentata</i>	Plant: - increased biomass under drought stress conditions, enhanced activity of the enzymatic antioxidant system, and enhanced nutrient uptake Microbes: - P solubilization, production of IAA, and ACC deaminase	[78]
<i>Trichoderma harzianum</i> , <i>Glomus</i> spp., <i>Pseudomonas fluorescens</i>	<i>Capsicum annuum</i>	- enhanced yield, higher activity of antioxidative, and defense enzymes	[79]

One of the major drawbacks of the application of bioinoculants is the fact that the number of bioinoculants tested in laboratory/greenhouse conditions fail in the field trials. This is mostly because microbes introduced to the environment have to compete for a niche with native microorganisms in order to attain sufficient abundance. The ability of introduced microbes to survive and thrive is variable and significantly depends on environmental conditions including temperature, rainfall, and soil type, as well as on interactions with the host plant and other organisms. A good example of this dependence is the field trial that showed that the promotion of plant growth by subtropical strains of *Azotobacter chroococcum* and *Azospirillum brasilense* was observed only when used in the same type of climate and not in the alpine region with a temperate climate [80]. Moreover, it was demonstrated that the high biodiversity of the native soil microbiome has a negative impact on the survivability of applied bioinoculants, i.e., there is a negative correlation between the diversity of the soil microbes and the survival rate of the introduced strain [81]. Therefore, when the native microbiome biodiversity is low, the chance for a new strain to thrive is higher which corresponds with better availability of nutrients and reduced competition among microorganisms for niche [82–84]. Moreover, several studies showed

that PGPM that promotes the growth of a particular plant species might not be beneficial for other species of plants. For example, fungi belonging to *Penicillium* sp. and *Trichoderma* sp. showed diversified effectiveness in enhancing the growth of varied wheat (*Triticum aestivum* L.) cultivars [85]. Similarly, the effect of inoculation of winter and spring varieties of oilseed rape (*Brassica napus* L.) with different strains of PGPM on the germination rate and growth of seedlings depended on the plant variety [86]. On the other hand, different strains of the same microbial species might differ significantly in their ability to promote plant growth and development. For example, Znajewska et al. [59] showed that seven *Trichoderma viride* isolates had various effects on winter rapeseed germination and growth promotion depending on the used strain.

Microorganisms colonize not only roots but also other plant tissues and organs including stems, leaves, flowers, seeds, and fruits. The aerial part of plants colonized by microbes is called the phyllosphere, whereas the rhizosphere is the soil adjacent to the root [87]. In contrast to the rhizosphere, the above-ground parts of plants are scarce in water and nutrients. Only a small number of microorganisms that reach the surface of the plant will land on beneficial spots and will have conditions to survive [88]. As a consequence, the number of microorganisms living in the rhizosphere is much higher than in the phyllosphere. Microbes are present at every stage of plant development, from seed to fully developed plant producing a new generation of seeds [89]. Some microorganisms live on the surfaces of plant organs, i.e., epiphytes whereas others are able to colonize the internal tissues of plants, i.e., endophytes [90,91].

Plant growth-promoting microorganisms stimulate plant growth and development through various direct and indirect mechanisms (Figure 1, Table 1). Production of phytohormones [92,93], nitrogen assimilation [94], solubilization, and mineralization of macro- and micro-elements [95,96], and modulation of the endogenous level of ethylene in plants tissues [97] are examples of direct mechanisms. Examples of indirect mechanisms are inhibition of pathogens growth through antibiosis [98], secretion of lytic enzymes [99], and competition, e.g., via siderophores production [100], induction/inhibition of plant genes expression [101], induction of plant immune response [102], and manipulation of plant microbiome composition [103]. This work aims to summarize the current knowledge about the interactions of plants with beneficial microbes, and how those interactions affect the overall health of the plant. For further development of environmental-friendly methods of plant cultivation, it is crucial to deeply understand the molecular mechanisms underneath (i) the recruitment of useful microbes by plants, (ii) the interactions among microorganisms, and (iii) the plant-microorganism interplay. The interactions between plants and microorganisms can be divided into three types, i.e., interactions are either neutral, negative, or positive in their effects on the host plant. This review focuses exclusively on positive interactions and mechanisms underneath those interactions. In this work, we also discuss the role of stringent responses in interactions between plants and microorganisms.

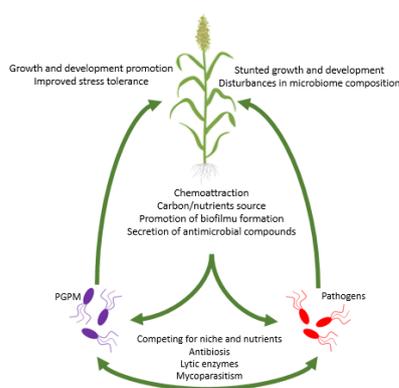


Figure 1. Multidimensional network of interactions between plants and PGPM, between plants and pathogens, and between PGPM and pathogens.

2. Rhizosphere and Root Exudates

The rhizosphere is defined as “the field of action or influence of a root”, i.e., it is soil adjacent to the roots which are influenced by root exudates that are the mixture of several compounds produced and secreted by roots [104]. The main components of root exudates are water, enzymes, amino acids, nucleotides, vitamins, organic acids, fatty acids, sugars, phenolic compounds, anions, volatile organic compounds (VOCs), polysaccharides, and proteins [105–112]. The composition of exudates varies depending on the plant species, and even phenotype; it changes during plant development [107,113] and it is dependent on environmental conditions, such as temperature [114], light [115], the amount of nutrients [116–119], and stress factors [120–122]. Moreover, the type and composition of soil can also affect the composition of root exudates [123]. For instance, plants that grow in soil deprived of nitrogen probably do not secrete extra amino acids or proteins to the rhizosphere [119]. Root exudates are also an important source of elements present in the soil. It was estimated that about 10–44% of carbon compounds [124] and about 10–16% of nitrogen compounds [125] synthesized by the plant is secreted to the rhizosphere. In legumes, the rhizodeposition of nitrogen is estimated between 4% and 70%, depending on the plant species [126].

The rhizosphere is the hotspot of plant–microorganism interactions. Interactions between those organisms have a direct influence on the availability of soil nutrients for plants [95,127–130] and on plant tolerance toward biotic and abiotic stresses [131–135]. Exudates are a rich source of carbon and other nutrients and, therefore, the abundance of microorganisms in the rhizosphere can be up to a hundred times greater than in the bulk soil [136]. Moreover, root exudates allow plants to communicate with rhizosphere microorganisms and affect their behavior through the secretion of various signaling molecules [137–140]. For instance, barley (*Hordeum vulgare* L.) in response to infection by the fungus *Pythium ultimum*, secretes increased amounts of organic and phenolic acids, which activates the expression of the *phlA* gene in the endophytic bacterium *Pseudomonas fluorescens* CHA0. Hydroxymethylglutaryl-CoA synthase encoded by the *phlA* gene is involved in the synthesis of DAPG (1,4-diacetylphloroglucinol) that has antifungal activity [98]. Zhang et al. [141] demonstrated the role of organic acids in root exudates of cucumber (*Cucumis sativus* L.) and banana (*Musa acuminata* Colla). The citric acid present in cucumber root exudates attracted *Bacillus amyloliquefaciens* (isolated from cucumber rhizosphere) and *B. subtilis* (isolated from banana rhizosphere). Moreover, it induced the formation of the *B. amyloliquefaciens* biofilm. Fumaric acid present in banana root exudates promoted biofilm formation of both tested strains. Biofilm is a coherent multicellular structure embedded in a self-produced extracellular matrix that can be formed on the surface of plant organs. Members of biofilm are better protected from environmental factors; their nutritional status is enhanced and, therefore, the survival rate of members of biofilm is much higher than that of single bacteria cells, as reviewed in [142]. Another example of a molecule allowing plant–PGPM communication is polyamines present in root exudates, which inform rhizospheric microorganisms about the presence of a potential host plant [143]. For instance, putrescine and its precursor arginine attract *Pseudomonas* sp. and trigger a lifestyle change, promoting attachment to the root and formation of biofilm [144]. However, the best-known example is the mechanism of communication between *Rhizobium* and legumes. Flavonoids secreted by plants activate bacterial *nod* genes lead to secretion by bacteria of the nod factor. The nod factor promotes the formation of nitrogen-fixing nodules in roots [145,146].

Root exudates serve as a chemoattractant, by which plants “recruit” microorganisms (Figure 1). Several studies showed that the composition of root exudates has an enormous effect on the composition of plant microbiome [147–152]. The composition of root exudates is specific for each plant species, which enables plants to attract a particular set of microbes [153]. Moreover, plants can secrete substrates that are available only for selected microbial groups or compounds that are toxic for certain groups of microorganisms in order to inhibit their growth [154]. A prominent example is the amino acid canavanine, which

is present in seeds and root exudates of legumes. Canavanine is toxic to a number of soil bacteria excluding rhizobia which possess the *msiA* gene encoding canavanine exporter that warrants canavanine resistance [155]. Mardani-Korrani et al. [156] demonstrated that canavanine is secreted by *Vicia villosa* Roth, significantly decreased the diversity and changed the composition of microbial communities in soil. The presence of canavanine caused an increase in the abundance of Firmicutes and Actinobacteria and decreased the number of Proteobacteria and Acidobacteria. Another example of the selective action of compounds present in root exudates is coumarin secreted by *Arabidopsis thaliana* (L.) Heynh. Coumarin selectively inhibits the proliferation of some pathogenic fungi, stimulates the growth of some *Pseudomonas* spp. and other microbes that belong to the PGPM group, and increases the bioavailability of iron by ferric ions reduction [157]. Coumarins are used by plants to increase the bioavailability of iron. Coumarins, such as scopoletin and esculetin, enable the mobilization of Fe from minerals in acidic and alkalic soil [158]. Moreover, the depletion of Fe in soils enhances the biosynthesis and secretion of coumarins in *A. thaliana* [157]. It is also worth noting that fungi also produce and secrete exudates that might affect other rhizosphere microorganisms. An interesting observation was made by Toljander et al. [159], who showed that arbuscular mycorrhizal fungi (AMF) affect the composition of bacterial community through mycelia exudates. Analysis of exudates produced by *Glomus* sp. showed that the main components are water, low molecular weight sugars, and organic acids. Moreover, it was shown that *Glomus* exudates inhibited the growth of several bacterial strains including opportunistic pathogens *Flavobacterium* spp. and increased the abundance of bacteria belonging to Gammaproteobacteria.

Root exudates are usually secreted without energy, mostly through diffusion, ionic channel, and vesicle transport. Among several transporters involved in the secretion of exudates by roots are ABC (ATP-binding cassette) transporters which transport lipids and flavonoids [160], and anion channels are involved in secreting carbohydrates [161]. Moreover, for the secretion of root exudates transmembrane proteins aquaporins (AQPs) that are related to the membrane reflection coefficient and root hydraulic conductivity seem to be of great importance, as reviewed in [162]. Aquaporins are present in endogenous and exogenous membranes of eukaryotes and prokaryotes and are responsible for symplastic transport of not only water but also low molecular weight compounds and non-charged molecules including urea, glycerol, hydrogen peroxide, ammonium ions, and some elements, e.g., silicon and boron, as reviewed in [163]. Interestingly, it was demonstrated that during ectomycorrhiza formation the expression of fungi *Laccaria bicolor* aquaporins significantly increased. Moreover, fungal aquaporins exhibit high permeability for NH_3 and, therefore, it was suggested that they are involved in the transfer of this compound from fungal cytoplasm to plant [164]. *Glycine max* L. noduline 26 aquaglyceroporin (GmNod26) is located in the symbiosome membrane in N_2 -fixing nodules and is a transporter of ammonia. The C-terminal domain of GmNod26 interacts with the main ammonia assimilatory enzyme, i.e., glutamine synthetase, and this probably supports the effective assimilation of fixed nitrogen [165,166]. The potential of root exudates to determine the composition of the rhizosphere microbiome is also important for the biodegradation of various soil pollutants. Environmental pollution is a serious global challenge and needs urgent development of effective methods of remediation. An interesting observation was presented by Janczak et al. [167,168] who showed that the presence of plants had a positive effect on bacterial, (i.e., *Arthrobacter sulfonivorans*, and *Serratia plymuthica*), and fungal, (i.e., *Clitocybe* sp. and *Laccaria laccata*), ability to degrade polymers including polylactide (PLA) and poly(ethylene terephthalate) (PET). The effectiveness of biodegradation also significantly depended on the species, i.e., the presence of *Salix viminalis* L. (willow) enhanced the level of biodegradation more significantly than the presence of *B. napus* and *Miscanthus x giganteus* J.M.Greef, Deuter ex Hodk., Renvoize (giant miscanthus). It was suggested that root exudates probably support the growth of microorganisms and/or root exudates can activate microbial genes involved in the biodegradation of plastics, such as intra- and extra-cellular depolymerases. The breakdown of long polymers into oligo-, di-,

and mono-mers enables uptake of those molecules by a bacterial cell which can be then utilized as a carbon and/or energy source [169]. Afzal et al. [170] reported that inoculation of Italian ryegrass (*Lolium multiflorum* Lam.) and birdsfoot trefoil (*Lotus corniculatus* L.) with alkane-degrading bacteria *Pantoea* ssp. and *Pseudomonas* sp. separately or in consortium resulted in higher biomass production by plants and bacterial consortium showed higher degradation ratio in comparison to single strain inoculants. The ability of these bacteria to degrade alkane was linked to the presence of genes encoding cytochrome p450 alkane hydroxylase (CYP153) and alkane monooxygenase (*alkB*). *Enterobacter ludwigii* possessing the CYP153 gene was able to degrade diesel fuel [171]. On the other hand, it was shown that the level of degradation of polycyclic aromatic hydrocarbon was reduced in the presence of ryegrass (*Lolium perenne* L.) root exudates [172] which suggest that plants might differ in their potential to enhance bioremediation potential of soil microorganisms. The PGPM are able to degrade various other compounds of different origins as a means for the promotion of plant growth and development. Allelochemical compounds secreted by plants can hinder the cultivation of other plant species in cropping systems. *Trichoderma harzianum* SQR-T037 was shown to degrade allelochemicals secreted by cucumber roots (4-hydroxybenzoic acid, vanillic acid, ferulic acid, benzoic acid, 3-phenylpropionic acid, and cinnamic acid). The use of strains able to biodegrade allelochemicals can ameliorate allelopathic stress in continuous cropping systems [173]. Among common soil contaminants, plant protection agents are of special interest since their persistence in the agricultural soil is high, and their concentration may increase with each application. Diuron, a phenylurea herbicide, has a mean half-life of 330 days. Inoculation of soil containing diuron with fungal endophyte *Neurospora intermedia* leads to degradation of 99% of diuron in the soil after 3 days. Moreover, the authors reported that this strain is able to degrade other phenylurea herbicides, e.g., fenuron, monuron, isoproturon, chlorbromuron, and chlortoluron [174]. Although organophosphorus pesticides are perceived as non-persistent, they are highly toxic for a wide variety of non-target organisms, including mammals and rhizospheric microbes. Tested strains of *T. harzianum* and *Metarhizium anisopliae* showed an ability to degrade a number of organophosphorus pesticides such as diazinon, profenofos, and malathion in a temperature range of 20–45 °C [175].

3. Microbiome and Holobiont

Plants provide a multitude of ecological niches for various organisms to thrive. All these organisms including bacteria, fungi, protists, and nematodes that live on the surface and inside tissues/organs of a certain plant form the plant microbiome [176]. Although each member of the microbiome might contain genes related to the promotion of plant growth and development, the expression of those genes is dependent on the composition of the whole microbiome, on the population dynamics of potential pathogens, and on environmental conditions [177]. For example, the consortium of six bacteria (*Arthrobacter nitroguajacolicus*, *Bacillus cereus*, *Bacillus megaterium*, *Bacillus mojavensis*, *Pseudomonas azotoformans*, and *Pseudomonas frederiksbergensis*) was much more effective in the protection of *Nicotiana attenuata* Torr. ex S.Watson (coyote tobacco) against fungal pathogens *Fusarium* sp. and *Alternaria* sp. than individual members of the consortium [178]. Analysis of *P. fluorescens* transcriptome in response to the presence of bacteria belonging to three different genera revealed significant differences in the transcription response of *P. fluorescens* to different competitors [179]. Moreover, another layer of microbiome complexity is added by the presence of microbial symbionts of the members of the plant microbiome. For example, plant-associated fungi are in symbiosis with bacteria, i.e., endofungal/endohyphal bacteria [180]. Interestingly, it was shown that endohyphal bacteria *Luteibacter* sp. significantly increases the production of indole-3-acetic acid (IAA) in fungi *Pestalotiopsis* sp. However, *Luteibacter* sp. is not able to synthesize IAA [181]. Viruses can also interact with the plant microbiome. *Dichanthelium lanuginosum* (Elliott) Gould (panic grass) grows in geothermal areas in consortium with its endophytic fungus *Curvularia protuberata*. When the fungus is infected with *Curvularia* thermal tolerance virus

(CThTV), soil temperature tolerance of panic grass increases from 40 °C to 65 °C [182,183]. Those results clearly show that other microorganisms present in soil strongly affect the PGPM potential to promote plant growth and development.

Although plants recruit a number of diverse microorganisms, they show preferences toward specific bacteria species. Analysis of seeds of medicinal plant red sage (*Salvia multiorrhiza* Bunge) collected at different locations revealed that there are no significant differences in the composition of the microbiome, whereas different plant species collected at the same location had significantly different microbiomes. This indicates that different species of plants exhibit a preference for specific groups of microorganisms [184]. Redford et al. [185] demonstrated the structure of microbial communities present on *Pinus ponderosa* Dougl. Ex C. Lawson needles are very similar regardless of geographic location. However, there are also examples of substantial differences in the microbiome of different cultivars of one plant species described in the literature. For example, Germida et al. [186] showed that root microbiomes of modern and older wheat cultivars were significantly different. Moreover, some microorganisms interact only with single plant species. For instance, a number of ectomycorrhizal fungi form mycorrhiza only with one species of a tree, e.g., *Suillus grevillei* and larch (*Larix* sp.) (as reviewed in [187]). Species of *Pinaceae* are the only hosts for the fungal genus *Rhizopogon* [188]. The most known example is the highly specialized relationship between legumes and rhizobia [189]. Wicaksono et al. [190], by studying bog ecosystems, found that microbiomes of vascular plants are less diversified than those of non-vascular plants including bryophytes. Specificity between host and microbes seems to be a plastic trait modulated by the environment [191]. The mechanisms underneath the preferences of the host plant toward a specific set of microorganisms are not well understood, but recently Salas-González et al. [192] showed that mechanisms involved in the maintenance of plant mineral nutrient homeostasis also contribute to microbiome assembly.

The composition of the plant microbiome is largely dependent on the phase of plant growth and development. The mature seed is colonized by microorganisms that were associated with the mother plant, (i.e., microbes were transferred vertically), and those microorganisms are the first members of the microbiome of a newly emerging plant [193]. During germination, microbes transferred vertically have an advantage in plant colonization over the microorganisms present in the soil. During plant development, new symbiotic microorganisms transferred horizontally, (i.e., from the soil), appear [136,194]. Interestingly, it was demonstrated that microbes transferred vertically usually inhabit the phyllosphere, while the rhizosphere and root are colonized by the microorganisms from the soil. A study on oak (*Quercus robur* L.) microbial inheritance showed that microbial composition of the phyllosphere was very similar to the composition of the embryo [195]. Sánchez-López et al. [196] showed that seed endophyte *Methylobacterium* sp. Cp3 was transferred via seeds across three generations of the plant *Crotalaria pumila* Ortega. Moreover, when *Methylobacterium* sp. Cp3 was inoculated to the soil at the time of *C. pumila*, flowering migration of bacteria from soil to seeds was observed. Moreover, the microbiome strongly differs among plant organs and tissues, i.e., the surface of the leaf is colonized by different microorganisms in comparison to the rhizosphere microbes [177]. A study on native and cultivated *Agave* species showed differences in bacterial taxa colonizing the rhizosphere, the phyllosphere, and the leaf and root endosphere. Interestingly, a composition of the fungal microbiome was affected mainly by the host plant biogeography [197]. Zarraindia et al. [198] demonstrated that below- and above-ground microbial communities of grapevine (*Vitis vinifera* L.) were significantly different. Moreover, the composition of microbiomes of leaves, grapes, and flowers was more similar to the composition of soil microbiomes than to each other. Similarly, in sugarcane (*Saccharum* sp.), clear differences in microbial taxa between organ types were observed. Interestingly, the microbiome composition of the young shoots formed from the underground ratoon was very similar to the microbiome of roots [199]. The phyllosphere is a hostile and dynamic environment. Microbes present on plant above-ground surfaces are subjected to irregular nutrient avail-

ability and changeable environmental conditions. The phyllosphere microbiome seems to be even more dependent on environmental conditions than the root microbiome [88,185]. It should be pointed out that the data regarding phyllosphere microbiomes other than leaf microbiomes is still rather limited. A study on the microbiome of apple (*Malus domestica* Borkh.) flowers showed that the most popular are bacteria belonging to the extremophilic phylum *Deinococcus-Thermus*. Moreover, the composition of the flower microbiome was dependent on the phase of apple flower development [200].

The composition of the plant microbiome is also strongly influenced by various environmental factors, such as climate, soil properties [201–203], water [204], and nutrient availability [205,206]. The adaptation of plant metabolism to environmental change is strongly supported by rapidly changing microbial communities [204]. Analysis of the lettuce (*Lactuca sativa* L.) microbiome showed that the composition of the phyllosphere microbiome is strongly dependent on the time of the year [207]. Drought is one of the most important stress factors significantly affecting not only plant growth and the yield of crops [208], but also the plant microbiome. Drought affects the microbiome directly because a low level of soil moisture inhibits the growth of several microorganisms. In drought conditions, plants recruit stress microbiomes, i.e., the most beneficial group of microbes allowing the plant to adapt to a particular set of environmental conditions. For instance, the abundance of Actinobacteria increased in drought-treated roots and the rhizosphere of 18 species belonging to *Poaceae*. The results suggest that although the microbiome is species-specific, drought caused a relatively conserved response in different hosts [209]. In drought stress conditions, an increase in the abundance of the rhizospheric drought stress-resistant bacteria in *Oryza sativa* L. was observed, mainly members of Actinobacteria and Chloroflexi, whereas the abundance of Acidobacteria and Deltaproteobacteria decreased [210]. Nelson et al. [211] reported enormous changes in microbial composition in forest soils after wildfires which occur more often due to climate change. As expected, an overall decrease in the abundance and biodiversity of bacterial and fungal communities was observed one year after the fire. Both the carbon and nitrogen cycle were found to be impaired not only by the loss of microbial taxa involved in geochemical cycles, (e.g., no expression of *nifA* genes in tested soils was detected), but also by the activity of viruses. The presence of plant pathogens has also a substantial effect on the microbiome (Figure 1). In *Gossypium hirsutum* L. (cotton) infected with the pathogenic fungus *Verticillium*, the abundance of arbuscular mycorrhiza fungi and plant growth-promoting bacteria (PGPB) was lowered [212]. A study on strawberries (*Fragaria x ananassa* Duchesne) infected with *Verticillium dahliae* and *Macrophomina phaseolina* showed that plants without symptoms of infection had a higher abundance of PGPB than plants with visible symptoms of infection. The microbiome of healthy plants includes more bacteria antagonistic or competitive towards pathogens [213]. Moreover, herbivores can shape the plant microbiome. Kong et al. [214] showed that whitefly infestation of *Capsicum annuum* L. (pepper) changed the overall microbiome composition. *Pseudomonas* spp. that are recruited by the plant to the rhizosphere microbiome increased the mortality of whitefly.

A particular part of the microbiome is the core microbiome which consists of those species of microbes that regularly and ubiquitously appear in the microbiomes of particular plant species. The concept of the core microbiome was first coined by a scientist involved in the Human Microbiome Project, with the goal to identify microbial taxa and/or genes that are shared by all or most humans [215]. Microbial taxa that are commonly found in a number of environments or host types can be assigned to a core microbiome. The most common approach to verifying whether a species belong to the core microbiome is to determine microbial groups that are shared among two or more microbiomes of a particular host in various environments [216]. For example, analysis of the *B. napus* rhizosphere microbiome grown in different conditions, i.e., the level of fertilization and the level of plant density, revealed that the core root microbiome of this plant is composed of microbes belonging to genera *Streptomyces*, *Cryocolla*, *Arthrobacter*, *Flavobacterium*, *Janthinobacterium*, *Serratia*, *Kaistobacter*, *Pseudomonas*, *Pedobacter*, *Agrobacterium*, *Burkholderia*, *Acidovorax*, *Erwinia*, and

Stentrophomonas [217]. Analysis of the composition of the microbiome of various plant species including *A. thaliana*, rice, sugarcane, grapevine, barley, and soybean has revealed that the core microbiome included microbes belonging to *Pseudomonas*, *Agrobacterium*, *Methylobacterium*, *Sphingomonas*, *Erwinia*, *Cladosporium*, *Conithyrium*, *Resinicium*, and *Fusarium* [177]. A special part of the core microbiome is a group of microorganisms called “hub microorganisms”. Those microorganisms strongly shape the composition of the microbiome through biotic interactions with host plants and other microbes. Microorganisms belonging to the hub species are called keystone species since they serve as mediators between the plant and members of the plant microbiome. Through the hub species, the host plant can selectively affect the composition of the associated microbiome. Removal of keystone species can result in the loss of interaction and a disturbance in the whole microbiome [218]. The analysis of the phyllosphere microbiome of *A. thaliana* showed that plant-parasitic oomycetes *Albugo laibachii* is a hub species that strongly affects the whole microbial community. As a consequence of infection with *A. laibachii*, high divergence between the composition of the microbiome of control and of infected plants was observed. Moreover, less variability among microbiomes of infected plants was shown [219]. In a study on corn (*Zea mays* L.) hub species, the elimination of *Enterobacter cloacae* from inoculum containing seven microbes resulted in a loss of a few other microbes from the microbiome. Removal of other bacteria from this system did not significantly change the microbial community which suggests that *E. cloacae* functions as a keystone species [220].

A far wider concept than microbiome is the concept of holobiont which was introduced in 1991 [221]. Currently, a holobiont is defined as an organism composed of the plant host and of all the microorganisms that are associated with that particular plant. Natural selection between the plant and microbes supports the system and its stability throughout the evolution of a holobiont. In a holobiont, intricate networks of interactions between microorganisms and plant host are observed (as reviewed in [177,218,222,223]). All the genes present in the holobiont, i.e., plant genes and genes in the microbiome, constitute the hologenome [224,225]. The concept of a hologenome suggests that plants’ adaptability to the environment is determined not only by plant genes but also by genes of microorganisms. Hologenomes are responsible for shaping the phenotype of holobionts in response to a particular set of environmental conditions [226].

4. Plant Immune System in Plant–PGPM Interactions

The plant immune system plays a key role in plant–microorganism interactions. It is crucial not only for controlling pathogenic microorganisms but also for balancing the homeostasis of the microbiome and for overseeing commensal microbes [227]. The prominent role in plant–PGPM interactions play patterns recognizing receptors (PRRs), which recognize conserved microorganisms-specific molecules referred to as pathogen-/microbe-associated molecular patterns (P/MAMPs), such as flagellin, lipopolysaccharides, antibiotics, and VOCs [228]. PRRs are transmembrane multimeric protein complexes located at the plasma membranes present in all plant organs and tissues. Plant PRRs are either surface-localized receptor kinases that contain ligand-binding ectodomain and intracellular kinase domain or receptor-like proteins that do not have any intracellular signaling domain. PRRs contain various ligand-binding ectodomains that allow for the recognition of a wide range of P/MAMPs [228] and activate pattern-triggered immunity (PTI) [229]. Activation of PTI via MAMPs inhibits intensive proliferation of most microorganisms via synthesis and secretion of low-molecular-weight compounds, e.g., phytoanticipins and proteins, e.g., defensins. Moreover, plants synthesize cuticles which lead to the thickening of the cell wall [227]. Some pathogens secrete effector molecules, which disturb PTI functioning and thus allow for the infection of the plant [222]. Effector-triggered immunity (ETI) is activated by recognition of pathogen effector proteins via intracellular receptors R proteins encoded by resistance genes (R genes) [230,231] and via nucleotide-binding leucine-rich repeat receptors (NLR) located in the cytoplasm [229]. ETI leads to the overproduction of reactive oxygen species (ROS) and ion fluxes. As a consequence, hypersensitive response

(HR) is activated which leads to apoptosis of infected plant cells that restrict the spread of infection [232].

Much less is known about the action of the plant immune system in the context of commensal microorganisms; however, there is some evidence that the plant immune system is crucial for microbiome assembly. Some strains of bacteria are able to modulate plant receptors, transcription factors, and molecules involved in the functioning of an immune system which allows for the colonization of plant tissues by other symbiotic microbes [233]. Moreover, some mechanisms used by the members of the microbiome to evade or suppress the plant immune system were also described. For example, in some symbiotic microorganisms, MAMP variants that do not activate plant immune response via PRRs have evolved. In addition, some commensal fungi are able to convert chitin into chitosan via deacetylation which induces a weaker immune response. MAMPs could be also degraded or sequestered by microbial proteases and other enzymes in order to evade recognition by PRR, as reviewed in [222]. It was also suggested that plants are able to actively ignore the presence of microbial commensals [234]. In *A. thaliana*, outer layers of roots low expression of PRRs and a lack of immune response in presence of pathogen- and commensal-derived MAMPs were reported. Neighboring cells harbor a high number of PRRs and show a rapid MAMP-triggered response [235].

5. Mechanisms Underneath PGPM–Plant Interactions

Plant growth-promoting microorganisms affect various aspects of plant growth and development. PGPM enhances the germination ratio [18,23,236], increases the elongation growth of the shoot and root [46,48,237], increases the biomass production [20,26,37], accelerates flowering [56,73], and increases the photosynthesis rate [27,42]. The examples of the mechanisms of action of plant growth-promoting fungi (PGPF) and bacteria (PGPB) are presented in Tables 2 and 3, respectively.

Table 2. Examples of mechanisms of plant growth promotion by PGPF.

Gene/Product	Function	Species	Reference
<i>aph</i> /acid phosphatase	- increased P availability via phosphates solubilization	<i>Aspergillus</i> , <i>Trichoderma</i> , <i>Penicillium</i>	[238,239]
<i>AMT1</i> ; <i>AMT2</i> ; <i>AAT9</i> /ammonium transporter; amino acid transporter	- improved N acquisition	<i>Tulasnella calospora</i>	[240]
<i>AQPF</i> /aquaporin	- transport of water to the host - enhanced drought stress resistance	<i>Glomus intraradices</i>	[241]
<i>Phy</i> /phytase	- increased P availability via solubilization of inositol	<i>Aspergillus</i> , <i>Trichoderma</i> , <i>Penicillium</i>	[238,239,242]
<i>acdS</i> /ACC deaminase	- degradation of ethylene precursor and protects against elevated ethylene levels - ameliorates stress effects and promotes root growth	<i>Trichoderma asperellum</i> , <i>Penicillium citrinum</i> , <i>Trichoderma gamsii</i>	[243]
<i>Hyd</i> ; <i>Qid</i> /hydrophobins	- allows for adhesion of hyphae to the surface of roots and protects hyphae against antifungal compounds - functions as MAMP (microbe-associated molecular pattern) and triggers plant response involved with symbiont recognition	<i>Trichoderma asperellum</i> , <i>Trichoderma harzianum</i>	[244,245]

Table 2. Cont.

Gene/Product	Function	Species	Reference
MST2/monosaccharide transporter2	- development of arbuscules - facilitates root colonization	<i>Glomus</i> sp.	[246]
Tex1/non-ribosomal peptided synthase	- synthesis of trichovirin II (peptaibol) which activates the plant immune system	<i>Trichoderma virens</i>	[247]
Thctf1/transcriptional factor	- regulates the synthesis of 6-pentyl-2H-pyran-2-one (6-PP) (VOC) which exhibits antifungal activity	<i>Trichoderma</i> sp.	[248]
Thph1; Thph2/cellulases	- cellulolytic activity - triggers plant immune system	<i>Trichoderma harzianum</i>	[236]
sidD/siderophores synthase	- synthesis of siderophores - improved Fe acquisition - defense against pathogens	<i>Trichoderma reesei</i> , <i>Trichoderma virens</i>	[249]
Sm1; Sm2; Ep1; Swo /cerato-platanins; swollenin	- fungal elicitors and upregulation of genes involved in JA signaling (modulation of the immune system) - swollenin disrupts the plant cell wall structure and enables penetration of the apoplast	<i>Trichoderma citrinoviride</i> , <i>Trichoderma virens</i>	[250–252]

Table 3. Examples of mechanisms of plant growth promotion by PGPB.

Gene/Product	Function	Species	Reference
2,3-butanediol dehydrogenase	- synthesis of 2,3-butanediol - growth promotion - induction of ISR	<i>Bacillus</i> sp., <i>Aerobacter</i> sp., <i>Serratia</i> sp., <i>Enterobacter</i> sp., <i>Klebsiella</i> sp.	[253]
<i>acdS</i> /ACC deaminase	- degradation of ethylene precursor and protects against elevated ethylene levels - ameliorates stress effects	<i>Azospirillum</i> sp. <i>Pseudomonas putida</i>	[254,255]
alkaline phosphatase	- increased P availability via phosphates solubilization	<i>Pseudomonas brassicacearum</i>	[253]
<i>bud</i> operon	- synthesis of acetoin and 2,3-butanediol - induction of ISR (induced systemic resistance) - increased drought tolerance	<i>Enterobacter</i> sp638	[256]
chitinase; glucanase	- defense against fungal pathogens	<i>Pseudomonas aureginosa</i> , <i>Pseudomonas veronii</i>	[257,258]
exoprotease	- N acquisition - protection against pathogens	<i>Pseudomonas brassicacearum</i>	[253]

Table 3. Cont.

Gene/Product	Function	Species	Reference
<i>fur</i> /transcription factor	- modulates gene expression encoding Fe transporter - Fe acquisition	<i>Pseudomonas brassicacearum</i>	[253]
<i>gcd</i> /pyrroloquinoline quinone (PQQ)-dependant dehydrogenase	- production of gluconic acid - P acquisition	<i>Pseudomonas fluorescens</i> F113, <i>Erwinia herbicola</i> , <i>Enterobacter intermedium</i>	[253]
<i>hcnABC</i> /HCN synthase	- protection against pathogens	<i>Pseudomonas fluorescens</i> . <i>Pseudomonas aeruginosa</i> , <i>Pseudomonas chlororaphis</i>	[259]
<i>ilvHI</i> ; <i>ivlC</i> /acetoxyacid synthase; ketol-acid reductoisomerase	- synthesis of secondary metabolites including antibiotics - induction of ISR	<i>Bacillus subtilis</i>	[253]
<i>ipd</i> ; <i>ppd</i> /indole-3-pyruvate decarboxylase; phenylpyruvate fenylopirogronian decarboxylase	- synthesis of IAA - promotion of root growth	<i>Azospirillum brasilense</i> Sp245, <i>Enterobacter cloacae</i> UW5, <i>Enterobacteriaceae</i>	[260–262]
<i>nagA</i> /N-acetylglucosamine-6 phosphate deacetylase	- chitinase-like protein and defense against fungal pathogens	<i>Pseudomonas brassicacearum</i>	[253]
<i>nif</i> /nitrogenase	- nitrogen assimilation	<i>Azospirillum</i> , <i>Burkholderia</i> , <i>Rhizobium</i> , <i>Bradyrhizobium</i> , <i>Mesorhizobium</i> , <i>Delftia</i> , <i>Stenotrophomonas</i> , <i>Rhizobium</i> , <i>Brevundimonas</i> , <i>Variovorax</i> , <i>Achromobacter</i> , <i>Novosphingobium</i> , <i>Comamonas</i>	[263–266]
<i>phl</i> operon	- production of antibiotic 2,4-diacetylphloroglucinol - induction of ISR	<i>Pseudomonas fluorescens</i> F113, <i>Pseudomonas protegenes</i> CHA0	[267]
<i>phyC</i> /phytase	- increased P availability via solubilization of inositol	<i>Pseudomonas brassicacearum</i>	[253]
<i>rhb</i> ; <i>rhtA</i> /siderophore synthase; mebrane Fe-regulated receptor	- production of rhziobactin (siderophore) and Fe acquisition - Fe uptake regulation	<i>Sinorhizobium meliloti</i>	[268]
<i>ribC</i> /riboflavin synthase	- growth promotion - defense against pathogens via ISR - upregulation of pathogenesis-related genes	<i>Pseudomonas yamanorum</i>	[269]
<i>yecA</i> ; <i>speB</i> /polyamine permease; agmatinase	- synthesis and/or secretion of polyamines - lowers ethylene level in root cells - modulation of expansin genes expression - promotion of root growth - increases tolerance to low pH, oxidative and osmotic stress	<i>Bacillus subtilis</i> OKB105	[270]

Several mechanisms underneath the promotion of plant growth and development by microorganisms are employed by both bacteria and fungi for example degradation of ethylene via ACC deaminase, production of phytohormones, and solubilization of various soil compounds to increase the bioavailability of nutrients (Tables 2 and 3). For sure the mechanism of greatest importance is the fixation of atmospheric nitrogen via

nitrogenase, a mechanism that is specific to some specialized groups of prokaryotes (as reviewed in [271,272]). On the other hand, the fungi-specific mechanisms that allow for the promotion of plant growth and development includes the production of hydrophobins, swollenins, and peptaibols (please see the section *Trichoderma*-plant interaction—a case study, for details).

5.1. Plant Antioxidant Defence System

One of the best-known mechanisms to improve plant growth and development by PGPM is the modification of the level of antioxidants including antioxidative enzymes, e.g., superoxide dismutase (SOD), ascorbate peroxidase (APX), peroxidase (POD), catalase (CAT), glutathione reductase (GR), and non-enzymatic antioxidants, e.g., proline, glutathione (GSH), ascorbic acid, carotenoids, and phenolics [25,273–277]. Islam et al. [278] demonstrated that inoculation of *Vigna radiata* (L.) R. Wilczek with *Bacillus cereus* Pb25 increased dry biomass and yield in salt stress conditions. Salt-induced oxidative damage was reduced by enhancing the activity of plant POD, SOD, and CAT and by increasing proline content in plants. Inoculation of *O. sativa* with *Bacillus pumilus* increased the activity of rice catalase and superoxide dismutase in salt stress conditions. Moreover, inoculation of rice with *B. pumilus* promoted the synthesis of photosynthetic pigments and proline [275]. Accumulation of phenols and proline was observed in cucumber inoculated with arbuscular mycorrhizal fungi in salt conditions [279]. A potato co-inoculated with *T. viride* and plant pathogen *Alternaria solani* showed improved redox homeostasis via increased activity of CAT and SOD, and enhanced concentration of free phenolics. Moreover, co-inoculation with *T. viride* and *A. solani* resulted in increased H₂O₂ production which induced the expression of plant defense genes [274]. Chen et al. [25] reported increased salt stress tolerance in maize after inoculation with *B. amyloliquefaciens* SQR9. Inoculated plants showed a reduced level of Na⁺, a higher glutathione content, a higher concentration of soluble sugars, and enhanced activities of peroxidase and catalase. *B. amyloliquefaciens* enhanced chlorophyll content and promoted the overall growth of inoculated plants in comparison to control plants. In addition to the well-known elements of the antioxidant system, there are also other proteins exhibiting antioxidant activity, including small cysteine-rich proteins metallothioneins (MTs). MTs act as direct antioxidants since the reduced thiol groups (-SH) can be oxidized by ROS. MTs also serve as a donor of zinc and copper to other antioxidative enzymes [280,281]. Inoculation of rapeseed with fungal strains isolated from forest soil showed varied expressions of *B. napus* metallothioneins (*BnMT1*-*BnMT3*). *L. laccata* inoculated plants showed significant upregulation of *BnMT2* expression with a decrease in *BnMT3* transcripts [43].

5.2. Phytohormones

Some bacteria are able to synthesize and secrete phytohormones and thus regulate plant growth and development. For example, *B. subtilis* synthesizes auxins and gibberellins [282], and *A. brasilense* [283,284], *Peanibacillus polymyxa* [285], and *P. fluorescens* [286] produce cytokinins. Inoculation of *S. tuberosum* damaged by insect attack (beetle *Leptinotarsa decemlineata*) with *B. subtilis* 26D led to increased concentration of zeatin-riboside but not of abscisic acid (ABA) and indole acetic acid (IAA). The inoculation of potatoes with *B. subtilis* increased the mass of roots [287]. In the culture of *Bacillus aryabhatai* abscisic acid, indole acetic acid, cytokinins, and gibberellic acids were detected. Soybean inoculated with these bacteria produced more IAA, jasmonic acid, and some gibberellic acids. Moreover, inoculated plants displayed increased tolerance to heat stress possibly due to the ABA-induced closure of stomata [288].

Although different stressors affect plant organisms in various ways, most of them lead to increased ethylene production in plants. Weak stress factors can cause small overproduction of ethylene which leads to the activation of plant stress-related genes. Long periods of stress and severe stressors cause a high level of ethylene production, which might lead to senescence, chlorosis, and organ abscission [136]. Some PGPM are able to

lower the level of ethylene through secretion of ACC deaminase, i.e., the enzyme that breaks down ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC). Inoculation of plants with microbes producing ACC deaminase effectively increased the plant resistance to stress caused by fungal pathogens [289], nematodes [290], and several abiotic stresses such as flooding [291], drought [135], salination [133], heavy metals [292], and toxic contaminants [134]. For example, inoculation of pearl millet seed with ACC deaminase-producing *B. amyloliquefaciens* increased plant growth in drought stress via increasing the level of enzymatic and non-enzymatic antioxidants [272]. Isolated from *Brassica rapa* L. rhizosphere bacteria belonging to *Pseudomonas* sp. improved biomass and yield of *B. rapa*. The positive effect of analyzed strains on *B. rapa* is possibly due to the production of IAA, ACC deaminase, and siderophores [95].

5.3. Availability of Micro- and Macronutrients

In most terrestrial ecosystems, nitrogen is the major nutrient limiting plant growth. PGPMs might increase the pool of nitrogen available for plants through various mechanisms. It is estimated that in nature more than 60% of fixed nitrogen is a result of biological nitrogen fixation [272]. A well-known example is the *Rhizobia* present in root and stem nodules of legumes that is able to reduce N_2 to ammonia. There are also other symbiotic, plant-endophytic, and free-living bacteria able to fix molecular nitrogen, including bacteria belonging to *Frankia*, *Cyanobacteria*, *Azotobacter*, *Bacillus*, and *Azospirillum*, as reviewed in [293]. The Co-inoculation of beans with *Rhizobium phaseoli* and bacteria belonging to *Bacillus* and *Pseudomonas* improved plant growth by enhancing the total content of nitrogen in plant tissues more efficiently than inoculation with *R. phaseoli*. Only [127]. Hungria et al. [130] reported that the co-inoculation of soybean seeds with *Azospirillum* and *Bradyrhizobium* significantly enhances the yield without any input of nitrogen fertilizers. Several lines of evidence showed that rhizobia are susceptible to drought-stress and the efficiency of N_2 -fixation dramatically declines in low-water conditions [294]. For example, co-inoculation of a common bean with *Rhizobium tropici* and two strains of *P. polymyxa* more effectively increased nitrogen content and promoted plant growth than inoculation with *Rhizobium* only especially in drought conditions [295].

Phosphorus is also considered as element limiting plant growth in most ecosystems. Although phosphorus is an abundant element in ecosystems, most of it is not bioavailable [296]. There is a group of microbes, phosphate solubilizing microorganisms (PSM), that are able to increase the available fraction of phosphorus for plants via solubilization and mineralization mediated by secretion of organic acids, phosphatases, protons, and exopolysaccharides [297]. Red clover (*Trifolium pratense* L.) inoculated with phosphate solubilizing fungi *Penicillium albidum* showed a significant increase in root biomass. In soil inoculated with fungi, the phosphatase activity was 1.5-fold higher than in the non-inoculated soil [129]. In soil inoculated with *Burkholderia* sp., *Gluconobacter* sp., and *Pseudomonas striata*, higher activity of dehydrogenase and phosphatase and a higher level of available P were detected. *Vigna unguiculata* (L.) Walp. grown in inoculated soil had noticeably higher biomass and yield than plants grown in non-inoculated soil. Moreover, tested microorganisms enhance uptake not only of phosphorus but also of nitrogen [298]. Inoculation of *T. aestivum* with *Serratia marcescens* enhanced plant growth and nutrient uptake (P, N, and K) in low temperatures. The ability of tested bacteria to solubilize P decreased at low temperatures [299].

Soil minerals, such as feldspars and micas, are the most common form of potassium in soils. Up to 90–98% of soil potassium is present in a form unavailable for plants [300]. By secretion of organic acids and capsular polysaccharides, some PGPM are able to solubilize potassium rocks, e.g., bacteria belonging to *Acidithiobacillus*, *Bacillus*, *Pseudomonas*, *Burkholderia*, and *Peanibacillus* [301]. Ali et al. [302] reported that inoculation of potatoes with K-solubilizing *B. cereus* resulted in significantly improved plant growth and yield. Moreover, the content of K in potato tubers and the content of N, P, and K in leaves was higher in comparison to control plants. Inoculation of ryegrass with *Mesorhizobium* sp.,

Peanibacillus sp., and *Arthrobacter* sp. isolated from canola rhizosphere improved biomass and yield. The content of available K in soil was much higher and resulted in increased K content in plants [303]. Basak and Biswas [304] demonstrated that treatment of waste mica with *Bacillus mucilaginosus* led to the transformation of K forms into water-soluble forms. This had a positive effect on K uptake and biomass of sudan grass (*Sorghum vulgare* Pers.). Similar effects were observed by Raji and Thangavelu [305], who analyzed the effect of inoculation of tomato (*Lycopersicon esculentum* L.) grown in Alfisol and Vertisol soils with *B. subtilis*, *B. cereus*, *Bacillus licheniformis*, and *Burkholderia cenocepacia*. Inoculated plants showed higher K content in tissues and improved growth.

The deficiency of microelements, including copper (Cu), iron (Fe), zinc (Zn), and manganese (Mn), is also a prominent factor that negatively affects plant health. In calcareous soils (widespread in arid and semiarid regions of the world), the high content of calcium carbonate which acts as a buffer and maintains a pH above 7.5, is correlated with decreased bioavailability of Fe, Zn, and Mn [306]. Plants possess mechanisms allowing them to increase amounts of bioavailable microelements in soils. For example, to facilitate Fe acquisition, plants secrete siderophores, organic acids, and flavonoids [307], whereas the amount of bioavailable Zn is increased by the secretion of organic acids, such as propionic acid, formic acid, lactic acid, citric acid, succinic acid, malic acid, oxalic acid, and gluconic acid as well as by secretion of siderophores, as reviewed in [308]. A tomato grown in hydroponic culture with the addition of soil minerals in Cu-deficient conditions showed increased biomass and Cu uptake after inoculation with *Trichoderma harzianum* SQR-T037 in comparison to non-inoculated plants. Interestingly, inoculation of a tomato with *T. harzianum* SQR-T037 grown in an Fe-deficient hydroponic culture with the addition of solid mineral increased the Fe content in plant tissue, but the biomass of seedling was unaffected. In addition, inoculation of tomatoes grown in Zn-deficient hydroponic conditions did not increase the biomass and the concentration of Zn in plant tissues was decreased. Those observations suggest that in element-deficient conditions fungi compete with plants for nutrients [309]. Rana et al. [128] showed enhanced yield and increased concentrations of Fe, Zn, Cu, and Mn by 13–16% in rice grains after inoculation with *Brevundimonas diminuta*, *Ochrobactrum anthropic*, and *Providencia* sp. Wheat inoculation with *Providencia* sp. significantly increased yield and the content of Fe and Cu in grains was 45% higher than in control plants. Singh et al. [310] reported that endophytic bacteria isolated from wheat, such as *B. subtilis*, *Arthrobacter* sp., *A. sulfonivorans*, and *Enterobacter hirae* exhibiting plant growth-promoting traits, enhanced Fe and Zn fortification as well as yield and dry/fresh weight in pot experiment and field conditions. Moreover, a decrease in phytic acid was observed in grains of wheat plants inoculated with endophytes. A field study on common bean and wheat fortification showed that inoculation with *A. brasilense* and *T. harzianum* significantly enhanced micronutrients, i.e., Fe, Mn, and Zn content in both tested plants [311]. Enhanced content of selenium was observed in lettuce inoculated with bacteria *Bacillus* sp., *Klebsiella* sp., *Acinetobacter* sp., and with fungus *Rhizopagus intraradices* in drought stress conditions. Results showed that plants inoculated with bacteria showed higher biomass production in comparison to plants inoculated with fungus, and *Klebsiella* sp. was the most effective in the induction of Se accumulation in lettuce. Moreover, tested microbes increased drought stress resistance, the chlorophyll and carotenoid content, and enhanced the level of antioxidant enzymes [312]. The ability of some PGPM to increase the content of macro- and micro-elements in different parts of plants is also important for human nutrition. Microelements deficiency (especially zinc and iron) is widespread all over the world. Biofortification, i.e., approaches to enhance the nutritional value of crops, with microelements in edible parts of plants, is the most promising approach to fight against microelements deficiency, as reviewed in [313–315]. Therefore, PGPM seems to be of crucial importance for both food quantity, i.e., enhanced plant yield and food quality, i.e., edible parts of plants with high content of minerals.

5.4. Direct Interactions of PGPM with Plant Pathogens

PGPM might directly interact with various plant pathogens. Through various mechanisms, including the production and secretion of antimicrobial metabolites, antagonisms, mycoparasitisms, and competing for niche PGPM can enhance plant biotic stress resistance. Cabrefiga et al. [316] reported an antagonistic interaction between *P. fluorescens* EPS62e and *Erwinia amylovora*, bacteria causing fire blight disease on pear trees (*Pyrus* sp.). *P. fluorescens* EPS62e did not produce antibiotics and required cell-to-cell contact with the pathogen in order to inhibit their growth on pear flowers and fruits. Interestingly, antagonistic activity was not shown when bacteria were grown in an Fe-rich medium, which suggested that the production of siderophores is responsible for the *P. fluorescens* EPS62e ability to inhibit the growth of *E. amylovora*. Inoculation of plants with antibiotic-producing microorganisms might lead to the suppression of various plant diseases. From the roots and rhizosphere soil of cucumber grown in soil inoculated with biocontrol agent *B. subtilis*, antibiotics surfactin and iturin A were extracted [317]. Bais et al. [318] showed that the biocontrol ability of *B. subtilis* against *Pseudomonas syringae* is tightly linked with the production of surfactin involved in biofilm formation on *A. thaliana* roots. *B. subtilis* mutant with a deletion in the surfactin synthase gene was unable to form biofilm and was ineffective in protection against *P. syringae* attack. Rhizospheric *S. plymuthica* HRO-C48 isolated from the rhizosphere of rapeseed produces antibiotic pyrrolnitrin and can protect plants against Verticillium wilt [319]. Kurze et al. [320] demonstrated that *S. plymuthica* HRO-C48 protects strawberries against fungal pathogens *V. dahliae* and *Phytophthora cactorum*. Moreover, the inoculation of strawberries with *S. plymuthica* promoted plant growth and improved yield. Inoculation of wheat seedlings with *Trichoderma* sp. resulted in an increase in plant resistance markers when plants were infected with *Fusarium* spp. Moreover, a decrease in IAA was observed. Biocontrol activity of *Trichoderma* was connected with the secretion of lytic enzymes and fungal elicitors as well as mycoparasitism [49]. An interesting observation was made by Chen et al. [321] who showed that *Pseudomonas piscium* isolated from wheat is able to alter histone acetylation in pathogenic *Fusarium graminearum* and, therefore, reduce the fungus level of virulence and mycotoxin production by the fungus. An identified compound secreted by *P. piscium*, i.e., phenazine-1-carboxamide, disturbs the activity of fungal histone acetyltransferase FgGcn5, responsible for the regulation of gene expression involved not only in virulence and the growth of the mycelium, but also in asexual and sexual reproduction and stress response.

5.5. Induction of the Plant Resistance by Microbial Elicitors

Although the use of living microorganisms is a potent tool in the development of sustainable agriculture, it has also numerous constraints due to legal regulations [322]. As an alternative to the living microbes and cell wall polymers (CWP) of bacteria, fungi can be employed as elicitors [323–325]. Elicitors trigger the immune response of the plant via numerous mechanisms including accumulation of lignin, antimicrobial enzymes, e.g., chitinases, glucanases, phytoalexins, and proteins related to the response to the presence of pathogens, guaiacol, and ribonuclease [326]. One of the efficient elicitors is chitin and its deacetylated derivative chitosan (N-acetylglucosamine subunits are linked by (1 → 4) -β bonds). For example, chitosan led to an increase in the systemic resistance in tomatoes and an increase in the plant resistance towards *Alternaria solani* and *Xanthomonas vesicatoria* [327]. Treatment of *Psammosilene tunicoides* with chitosan led to an increased expression of genes encoding antioxidant enzymes and transcription factors controlling stress-response genes. Moreover, the content of secondary metabolites terpenoid saponins increased [328]. The cost-effective and efficient source of elicitors are fungi belonging both to Ascomycota and Basidiomycota. Research by Nowak et al. [326] showed that (1 → 3) -α-D-glucooligosaccharides (GOS) obtained by hydrolysis of (1 → 3) -α-D-glucan from *Laetiporus sulphureus* induced the growth of wheat seedlings. Moreover, GOS caused the increase in the activity of CAT and APX, in the activity of chitinase, and higher activity of enzymes activating phenylpropanoid-producing pathways. Laminarin, a polysaccharide, consists of β-(1-3)-glucan with β-(1-6)-linkages

of 20–25 units isolated from brown algae, which is an example of elicitor belonging to β -glucans. Treatment of grapevine-cultured cells with laminarin led to calcium influx, an oxidative burst, and the induction of pathogen-related genes. Laminarin by the induction of plant resistance indirectly contributes to the reduction of the growth of *B. cinerea* and *Plasmopara viticola* on grapevine plants [329].

6. The Stringent Response in Plant–Microorganism Interactions

Among several plant mechanisms regulating growth, development, and the response to environmental factors, the stringent response is of particular interest. The stringent response was first discovered in *Escherichia coli* in response to amino acid starvation [330]. The hallmark of the stringent response is the accumulation of atypical regulatory nucleotides guanosine tetra- (ppGpp) and pentaphosphates (pppGpp) called alarmones that are responsible for pleiotropic adaptation to nutrient deficiency and stress factors [331,332]. Moreover, the bacterial stringent response through regulation of quorum sensing indirectly affects the formation of microcolonies and the development and functioning of biofilm [333]. Alarmones are synthesized from ATP/GTP or GDP by enzymes possessing active synthetase domain (SYNTH) and are hydrolyzed to GTP/GDP and pyrophosphate by enzymes containing active hydrolytic domain (HD). Gram-negative bacteria usually possess two separate enzymes, i.e., alarmones synthetase RelA and alarmones hydrolase SpoT. Gram-positive bacteria usually possess one bifunctional Rel protein [334,335]. RelA and SpoT belong to the long RSH (RelA/SpoT homologue), i.e., enzymes possessing HD and SYNTH domains. In bacteria, there are also short RSH, i.e., enzymes containing either SYNTH domain, small alarmone synthases (SAS) or HD domain, or small alarmone hydrolases (SAH), whereas in animals, to date only small alarmone hydrolases were identified (Mesh1—metazoan SpoT homologue) [336]. Alarmones regulate transcription, translation, and DNA replication, and trigger metabolic and physiological changes in response to unfavorable environmental conditions. Upon accumulation of alarmones, bacteria change their lifestyle from growth and proliferation to survival mode [335]. Sanchez-Vazquez et al. [337] demonstrated that in *E. coli*, the elevated (p)ppGpp level affected the expression of 757 genes five minutes after the induction of the stringent response and after another five minutes the expression of 1 224 genes was affected. Activation of the stringent response can be triggered by a deficiency of amino acids [330], fatty acids [338,339], iron [340], carbon [341], nitrogen [342], phosphorus [343], and by other types of stress, e.g., increased temperature [344,345], cell wall antibiotics, ethanol and acid treatments, superoxide stress [346], and alkaline shock [347].

The presence of (p)ppGpp in photosynthetic *Eucaryota* was confirmed in the algae *Chlamydomonas reinhardtii* [348]. In higher plants, RSH genes were identified for the first time in *A. thaliana* [349] and subsequently in other plant species, e.g., *Nicotiana tabacum* L. [350], rice [351], *Ipomoea nil* L. Roth [352], *Sueda japonica* Forssk. ex J.F. Gmel. [353], pepper [354], and non-vascular plants, e.g., *Physcomitrella patens* (Hedw.) Bruch and Schimp [355]. Plant RSH proteins are divided into three groups, i.e., RSH1, RSH2/3, and CRSH. All identified plant RSH proteins belong to the long RSH, i.e., possess both HD and SYNTH domains. In model plants, the *A. thaliana* SYNTH domain of RSH1 (AtRSH1) is inactive due to the substitution of conserved glycine residue required for its activity. AtCRSH does not possess a functional hydrolase domain and in AtRSH2/3, both SYNTH and HD domains are active [356]. In addition to HD and SYNTH domains, RSH possess chloroplast transit peptide [357], TGS (RSH1, RSH2/3), and ACT domains (RSH1) which were proposed to act as regulatory- or ligand-binding domains [358]. CRSH are the only proteins involved in alarmones metabolism that possess two EF hand motifs and are activated by Ca^{2+} ions [359]. The domain structure of RSH proteins is highly conserved across plant species. It is now widely accepted that in plants, the place of alarmones action are chloroplasts [360–363]. Alarmones act as regulators of plant development and growth, i.e., (p)ppGpp coordinate micro- and macro-elements redistribution during senescent [364]. They modulate the level of phytohormones [365], lipids [366,367], and

secondary metabolites [368] in chloroplasts. Moreover, alarmones promote the replication of plastidial DNA [364]. Plant *RSH* genes are differently expressed in presence of biotic and abiotic stress factors, which suggest that alarmones contribute to plant response in a number of stress factors, i.e., oxidative stress [369], nitrogen starvation [369,370], wounding, salination, drought, UV radiation, heat shock, heavy metals, and abrupt change from light to darkness [371]. Masuda et al. [372] showed that *RSH* probably play a role in plant reproduction, as the *AtCRSH* knockdown mutant produced smaller siliques and a lower number of seeds. An interesting observation was made by Ono et al. [373], who demonstrated an increased (p)ppGpp concentration in chloroplast upon a light-to-dark transition. The alarmones accumulation was due to higher activity of *CRSH* caused by elevated levels of Ca^{2+} in chloroplasts. As a consequence, the expression of plastidial genes is adapted to darkness. Interestingly, it was demonstrated that the accumulation of alarmones in plants leads to a decreased expression of genes involved in the defense system, which can lead to higher susceptibility to infections [365].

Plants are probably able to manipulate the level of alarmones synthesis in members of their own microbiome but also in pathogenic bacteria. Through modulation of (p)ppGpp production in bacteria, plants may be able to decrease virulence and inhibit the growth of pathogens. Nowicki et al. [374] demonstrated the activation of stringent response in *E. coli* cells by plant secondary metabolites isothiocyanates (ITC). ITC-induced stringent response in *E. coli* led to growth inhibition, disturbed transcription, and DNA replication. The induction of the *E. coli* stringent response may be the result of a direct interaction of ITC with cellular proteins. That idea is plausible since sulforaphane (one of the ITCs) inhibits the growth of numerous bacteria and recently potential target proteins of ITC were identified [375]. Mwita et al. [376] showed that the expression of *SasA* (short alarmone synthase) of PGPB *Bacillus atrophaeus* UCMB-5137 is considerably upregulated by maize root exudates. Further implications of observation on these bacteria metabolisms need, however, further evaluation. On the other hand, inoculation of plants with PGPB can affect plant *RSH* gene expression; however, the data are scarce. Dąbrowska et al. [377] demonstrated that *B. napus* inoculated with *S. plymuthica* and *Serratia liquefaciens* exhibited elevated mRNA levels of *BnRSH1* in cotyledons and roots, whereas inoculation with *Massilia timonae* increased *BnRSH1* expression only in roots. Moreover, *S. plymuthica* seemed to affect also the expression of *BnRSH2* and *BnRSH3* in cotyledons and roots. The relative transcript level of *BnCRSH* was elevated in cotyledons in presence of *S. plymuthica* and *S. liquefaciens*. Inoculation of canola grown in salt-stress conditions with endophytic *Pseudomonas stutzeri* ISE12 significantly increased mRNA levels of *BnRSH1* and *BnRSH3* in roots in comparison to non-inoculated plants grown in salt stress [34]. Moreover, Givens et al. [350] observed a 10-fold increase in *RSH2* protein level in *N. tabacum* after infecting the plant with the bacterial pathogen *Erwinia carotovora*.

Microbes might directly and/or indirectly activate the stringent response in other microorganisms. A study on the effect of the pathogenic fungus *Rhizoctonia solani* on the rhizosphere microbiome of sugar beet (*Beta vulgaris* L.) showed that in several rhizobacteria, the expression of genes involved in (p)ppGpp metabolism is upregulated. It is not clear whether the activation of the stringent response in bacteria present in the rhizosphere is triggered directly by oxalic and phenylacetic acids secreted by *R. solani* or indirectly by signaling molecules in root exudates [378]. Interestingly, the *relA* and *relA/spoT* mutants of *Pseudomonas* sp. DF41 and *Pseudomonas chlororaphis* PA23, showed increased antifungal activity against *Sclerotinia sclerotiorum*. All mutants produced an increased level of antifungal antibiotic pyrrolnitrin, lipase, and protease in comparison to wild-type bacteria. The lack of (p)ppGpp led also to reduced transcription of *rpoS* [379,380]. Selin et al. [381] showed that expression of *rsmZ*, *rsmE*, and *rsmA*, i.e., elements involved in the regulation of several processes such as virulence, motility, and biocontrol abilities, was regulated via the stringent response in *P. fluorescens*, a PGPB inhibiting the growth of a number of pathogenic fungi including *S. sclerotiorum*. Takeuchi et al. [382] reported that a mutant of *P. fluorescens* CHA0 lacking the ability to synthesize alarmones, produced significantly fewer antibiotics and

had lower biocontrol activity against *P. ultimum*. Moreover, the ability of the tested mutant to colonize cucumber roots, both in the presence and absence of *P. ultimum*, was reduced possibly due to impaired motility. The stringent response was found to strongly influence the production of antibiotics also in *Streptomyces* which are common members of the plant microbiome. Ochi [383] reported that *rel* mutant of *Streptomyces antibioticus* showed induction of phenoxazinone synthase, an enzyme involved in the production of actinomycin. Interestingly, this mutation did not affect the activity of another enzyme participating in the biosynthesis of actinomycin, i.e., kynurenine formamidase. Moreover, *RSH* genes regulated the morphological and physiological differentiation of *Streptomyces clavuligerus*; the lack of (p)ppGpp affected spore formation [384].

Recent studies showed that the stringent response may play a crucial role in the interaction between legumes and rhizobia. At the beginning of the interaction, legumes produce antimicrobial compounds that lead to nutritional, osmotic, and oxidative stress in rhizobia [385–387]. Based on the literature, it might be hypothesized that in order to survive these unfavorable conditions, rhizobia activates the stringent response. Soybean inoculated with the *rsh* knockout *Bradyrhizobium diazoefficiens* formed smaller nodules than those present in plants inoculated with wild-type *B. diazoefficiens*. Moreover, the biomass of plants inoculated with mutant bacteria was smaller in comparison to wild-type bacteria, but still higher than the biomass of non-inoculated plants. Those results suggest that the lack of alarmone signaling altered nodulation and, as a consequence, decreased N₂ fixation. Interestingly, in plants co-inoculated with wild-type bacteria and the *rsh* mutant in equal proportion, only 26% of nodules were infected by mutant bacteria. This observation strongly suggests that the stringent response is crucial to win the competition for a niche with other rhizobia [388]. In the early phase of nodulation, establishing a symbiotic relationship between rhizobia and legumes requires plant-bacteria signaling that allows the recognition of bacteria by the host. It was shown that *relA* mutant of *Sinorhizobium meliloti* failed to form nodules on *M. sativa* due to disturbed stringent response, but remarkably the nodulation of *Medicago truncatula* Gaertn. was successful. The N₂ fixation capacity of mutant bacteria was reduced in comparison to the wild type. It is not clear why there is a difference in nodulation between those two *Medicago* species; however, it might be hypothesized that different plants influenced bacterial stringent response at different stages of invasion [389]. Another study also found that *S. meliloti* mutant unable to synthesize (p)ppGpp did not establish a symbiotic relationship with *M. sativa*. The *relA* mutant of *S. meliloti* produced more succinoglycan, an exopolysaccharide needed for colonization of the host, than the wild-type bacteria [390]. The inactivation of *relA* in *Rhizobium etli* caused nodules on *P. vulgaris* form, but the level of nitrogen fixation was significantly reduced. Mutants showed significantly lower expression of *rail* and *cinI* genes which encode regulators of quorum sensing in rhizobia [391]. Calderón-Flores et al. [392] reported that in *P. vulgaris* inoculated with *R. etli*, the *rsh* mutant nodulation and nitrogen fixation were disturbed. Qiu et al. [393] demonstrated that the addition of water-soluble humic materials into inoculum containing *Sinorhizobium fredii* significantly downregulated *RSH* expression, increased survivability of bacteria in soil, and promoted rhizoplane colonization of *Glycine max* (L.) Merr.

The stringent response is also a significant mechanism contributing to the virulence of various plant pathogens. A study on *E. amylovora* showed that cells of *relA* and *relA/spoT* mutants were significantly longer both in nutrient-rich and nutrient-limited conditions in comparison to the wild type. Moreover, it was demonstrated that the proliferation rate of *relA/spoT* mutant in pear fruits was 1000 times slower than the proliferation rate of the wild type. In minimal medium double, the *relA/spoT* mutant was unable to grow. Small-sized cells are more resistant to stress, and bigger *relA/spoT* knockouts are unable to survive on plant surfaces. It seems that (p)ppGpp are important regulators of cell growth in *E. amylovora* during plant infection [394]. A similar observation was made for *P. syringae*, one of the most common plant pathogens. *P. syringae* single (*relA*) and double (*relA/spoT*) knockout mutants grown on nutrient-rich medium were slightly bigger

in comparison to the wild-type bacteria. An *in vivo* study demonstrated that *relA/spoT* mutants, even though they had bigger cells, were unable to survive on the surface of a tomato leaf. These findings suggest that the stringent response is a crucial element of plant surface colonization [395,396]. A great induction of *relA* and *spoT* genes in gram-negative bacterium *Pectobacterium atrosepticum*, able to degrade plant cell walls, was observed when bacteria were grown in high-density culture in carbon-deficient media [397,398]. Zhang et al. [399] reported that the *Xanthomonas citri* double knockout *spoT/relA* mutants showed a significant decrease in pathogenicity and inhibited growth in planta. Interestingly, the deletion of only the main alarmone synthase in the *X. citri relA* did not affect the virulence of the bacterium.

Several lines of evidence showed that the stringent response plays a crucial role in the adaptation of bacterial growth and metabolism to nutrient-limited conditions. The mentioned studies above show the importance of the stringent response for the establishment of plant–PGPM interactions and proper functioning of the plant microbiome. We hypothesize that the stringent response probably allows members of the microbiome to survive in unfavorable conditions during the first stages of interaction establishment. The data about the possible role of alarmone in an intricate network of interactions between plants and microorganisms, among members of microbiomes, and between PGPM and plant pathogens are rather limited. The possible crucial role of the plant and the microbial stringent response in the functioning of microbiomes is an exciting but rather overlooked research area that needs further experiments.

7. *Trichoderma*–Plant Interaction—A Case Study

Among several other microbes belonging to the PGPM group, fungi from the genus *Trichoderma* are of great interest. Adaptability to unfavorable environmental conditions and the ability to utilize many different substrates as nutrients determine the ubiquitous occurrence of fungi belonging to *Trichoderma* in soils. It is estimated that one gram of soil contains 10–10³ CFU (colony-forming unit) of fungi belonging to *Trichoderma* [400,401]. It was estimated that there are around 438 species in the genus *Trichoderma*, grouped into 10 phylogenetic lineages: *Brevicompectum*, *Deliquescens*, *Harzianum*, *Hypocreanum*, *Longibrachiatum*, *Polysporum*, *Psychrophilum*, *Semiorbis*, *Stromaticum*, and *Viride* [402].

Through interaction with plant fungi belonging to *Trichoderma* gains, a convenient niche for growth and development since root exudates are a rich source of carbon and other nutrients. The presence of fungi belonging to *Trichoderma* enhances growth and increases yield [403,404], improves uptake of nutrients by plants [405,406], and leads to a higher vigor and germination ratio of seeds [407,408]. In addition, fungi belonging to *Trichoderma* increase the level of photosynthesis [409], the level of amino acid synthesis [410], the level of transpiration [411], and the water content in tissues in drought conditions [412]. Fungi from the genus *Trichoderma* can colonize the roots of mono- [56,57,413] and dicots [58,131,132] and when plants are grown in acidic soils [414], alkaline soils [415,416], and soils contaminated with heavy metals [417,418]. *Trichoderma* are potential symbionts of non-mycorrhizal plants belonging to *Brassicaceae* [59], *Chenopodiaceae* [302], *Caryophyllaceae* [419], *Polygonaceae* [420], and others. Recently, marine isolates of *Trichoderma* have been identified [421–425], which have the potential to serve as plant growth-promoting fungi for plants grown in saline soils [426]. Several mechanisms have been shown to contribute to the promotion of plant growth and development by fungi belonging to *Trichoderma*. Colonization of plants by *Trichoderma* changes host proteome [413] and secretome [427], affecting the level of synthesis of phytohormones [428] in soluble sugars [409] and phenolic compounds [173,429]. The inoculation of *A. thaliana* seedlings with *Trichoderma virens* and *Trichoderma atroviride* increased biomass production and promoted lateral root growth. Mutations in plant genes involved in auxin transport and signaling, i.e., *AUX1*, *BIG*, *EIR1*, and *AXR1* caused reduced stimulation of root growth and development by tested *Trichoderma* isolates [92]. Fungi belonging to *Trichoderma* compete with pathogens for ecological niches and nutrients, which efficiently limits the growth of pathogens. Secreting

antibiotics, siderophores, a range of volatile and non-volatile metabolites (n-alkanes, cyclohexane, cyclopentane, esters, alcohols, sulfur-containing compounds, pyrane, and benzene derivatives), and through mycoparasitism fungi belonging to *Trichoderma*, protect plants against various pathogens, such as *R. solani* [430–432], *Rhizopus oryzae* [433], *Fusarium* spp. [434,435], *Alternaria alternata* [436], *S. sclerotiorum* [432,437], *Botrytis cinerea* [438,439], *Pythium* spp. [433], and *Ustilago maydis* [440]. Several secondary metabolites produced by fungi belonging to *Trichoderma* peptaibols seem to be of great importance for *Trichoderma* biocontrol activity. Peptaibols are amphipathic polypeptides composed of 5–10 amino acids with molecular masses between 500 and 2200 Da. These non-ribosomally synthesized polypeptides contain not only typical amino acids but also non-proteinogenic amino acids and α -aminoisobutyric acid. Peptaibols are synthesized not only by fungi belonging to *Trichoderma* but also by other soil-born fungi as well as by plant-pathogen fungi [441,442]. Several lines of evidence have confirmed that peptaibols exhibit antibacterial and antifungal properties. *Trichoderma pseudokoningii* produces trichokonin VI that induces apoptotic cell death in *F. oxysporum* [443]. Trichokonins A produced by *Trichoderma longibrachiatum* damages the cell membrane of Gram-negative pathogenic bacteria *Xanthomonas oryzae* pv. *Oryzae*, leading to a significant reduction of the pathogenicity of these bacteria [444]. The same inhibitory effect was observed for several other peptaibols produced by various *Trichoderma* species against a range of plant pathogens, e.g., *B. cinerea* [445], *Septoria tritici* [446], *A. solani*, and *R. solani* [447]. Moreover, it was also demonstrated that peptaibols can act against viruses. Luo et al. [448] showed that trichokonins isolated from *T. pseudokoningii* induces resistance of tobacco against the tobacco mosaic virus probably via induction of reactive oxygen species and phenolic compound production. Peptaibols isolated from *T. virens* might act as elicitors and induce a defense response in cucumber against pathogenic bacteria *Pseudomonas syringae* pv. *lachrymans* via up-regulation of hydroxyperoxide lyase, phenylalanine ammonia lyase, and peroxidase gene expression. In addition, *T. virens* mutant *tex1* lacking one of the non-ribosomal peptide synthetases was less effective in the inhibition of *P. syringae* pv. *lachrymans* growth [247]. It should be pointed out that high concentrations of peptaibols might have a negative impact on the growth of plants, as shown for peptaibols produced by *Trichoderma reesei* and their negative effect on *A. thaliana*. However, peptaibols at lower concentrations are still sufficient to inhibit the growth of plant pathogens with no adverse effect on plant growth [449].

Moreover, some strains of *Trichoderma* can induce ISR (induced systemic resistance) and/or SAR (systemic acquired resistance) in the host plant through the secretion of fungal elicitors. Shores et al. [450] demonstrated that the treatment of cucumber with *T. asperellum* T203 activated ISR via the JA/ethylene signaling pathway. Inoculated plants were more resistant to *P. syringae* than non-inoculated control plants. Another study showed that soil inoculation with *T. harzianum* enhanced tomato defense against root-knot nematode (*Meloidogyne incognita*) by SAR activation and increased ethylene synthesis [132]. Inoculation of canola with *T. harzianum* TH12 triggered SAR and ISR defense mechanisms and decreased the severity of disease symptoms caused by *S. sclerotiorum* [132]. Changes in host cells caused by inoculation with *Trichoderma* are also visible in tissues distant from the penetration site. Yedidia et al. [451] demonstrated that the cell walls of cucumber root epidermis and cortical cells after *T. harzianum* inoculation were strengthened also beyond the penetration site. The activity of plant peroxidases and chitinases was upregulated by the presence of a fungus both in roots and leaves. These findings are in agreement with the fact that microbial invasion of host plant cells induces systemic resistance mechanisms. Huang et al. [452] reported that inoculation of cucumber with *T. harzianum* SQR-T37 significantly promoted growth as well as suppressed the damping off disease caused by *R. solani*. It was shown that the main mechanism of biocontrol was mycoparasitism. Between the pathogen and *T. harzianum* SQR-T37, a direct interaction was observed. The hyphae of *T. harzianum* were densely coiled, and hooks and appressorium-like bodies were formed. As a consequence, the cell walls of *R. solani* were broken and leakage of cytoplasm was noted.

Fungi belonging to *Trichoderma* are able to colonize plants due to the mechanisms allowing the recognition and the adhesion to the surface of the root (Figure 2). Moreover, these fungi are able to penetrate the root tissues and suppress the plant's immune system in order to avoid strong responses from the host, as reviewed in [453,454]. The plant's immune system recognizes *Trichoderma* MAMPs, including swollenin [250], alamethicin [455], xylanase [456], cellulases [457], and polygalacturonase [458]. Plant responses to MAMPs are quick and transitional in the early stages, they involve ion level fluctuation, overproduction of ROS, nitric oxide, and ethylene [459]. Later stages involve the production of callus wall and antifungal compounds and, as a consequence, further penetration of the plant by hyphae is stopped [429,460]. It was demonstrated that salicylic acid has a particular role in callus synthesis during the colonization of plants by fungi. In a *A. thaliana sid2* (salicylic acid induction-deficient2) mutant with a disturbed SA signalization, *T. harzianum* penetrated root vascular tissues whereas in wild-type plants, penetration of plants by fungi were restricted to outer root layers [460]. Inoculation of *Z. mays* with *T. virens* caused the reduction of plant secretome by 36%, which deprives plants of essential signaling molecules and proteins crucial for proper plant growth and development. At the same time, a fungus secretes similar compounds which do not activate the plant's immune system [427]. The ability to colonize plant tissues by *Trichoderma* is tightly linked with the fungal capacity to tolerate secreted plants' antimicrobial compounds [459]. An ABC transporter system is crucial for the resistance of *Trichoderma* to antifungal compounds secreted by plant pathogens. Deletion in the *Taabc2* gene in *T. atroviride* caused the loss of the ability of the fungus to protect the tomato against *P. ultimum* and *R. solani* attacks [461]. Another mechanism exploited by fungi belonging to *Trichoderma* is directly decreasing the synthesis of the antifungal compound. For example, Masunaka et al. [462] reported that inoculation of *Lotus japonicus* L. with *Trichoderma koningi* down-regulated the production of isoflavonoid vesitol, i.e., the main phytoalexin produced by lotus species. Fungi belonging to *Trichoderma* were found proficient in the degradation of allelochemicals secreted by plants which exhibit fungitoxicity to a number of fungi [173].

Adhesion of fungi belonging to *Trichoderma* to the surface of plants is mediated by hydrophobins, i.e., small, cysteine-rich hydrophobic proteins (Figure 2). Hydrophobins are synthesized by filamentous fungi. The amino acid sequence of hydrophobins is highly evolutionarily conserved. Hydrophobins are classified into two classes based on the arrangement of cysteine residues, differences in solubility, and physical properties. Hydrophobins form amphipathic monolayers at hydrophobic-hydrophilic interfaces. Those proteins are involved in the formation of aerial hyphae, fruiting bodies, and spores as reviewed in [463,464]. It was shown that class I hydrophobins produced by *T. asperellum* enabled adhesion to cucumber roots. The authors hypothesized that hydrophobins protect hyphae against antimicrobial compounds were secreted by the host during colonization [244]. Inoculation of tomato and cucumber with a *T. harzianum* mutant with a deletion in the gene encoding hydrophobin showed that the mutant fungi were able to colonize the roots of both plants; however, the lateral roots were significantly shorter than those present in plants inoculated with the wild-type fungus [245]. Further penetration of roots by hyphae is possible due to fungal proteolytic enzymes, e.g., aspartyl protease (PapA) [465], and cellulolytic enzymes, e.g., endopolygalacturonase (ThPG1) [458], and arabinofuranosidases (Abf1, Abf2) [465] that allow for degradation of the plant cell wall. Another important element allowing *Trichoderma* for tissue penetration are swollenins (Figure 2), i.e., proteins possessing a cellulose-binding domain (CBD), similar to plant proteins—expansins. Swollenins disrupt the structure of the cellulose which results in changes to the plant cell wall architecture and the expansion of intercellular space [466]. Swollenins facilitate penetration of apoplast by the hyphae and give fungi an advantage during the competition for the niche with other microbes. Brotman et al. [250] reported that *T. asperellum* overexpressing swollenin showed a significantly improved ability to colonize cucumber roots, whereas swollenin knockout mutants showed a reduced ability to colonize roots. Moreover, it was found that the CBD domain acts as the MAMP, and can induce

plant defense against *B. cinerae* and *P. syringae*. Similarly, *T. atroviride* overexpressing the swollenin-coding gene *Taswo1* improved the colonization rate and enhanced the growth of tomatoes and peppers. Moreover, the induction of the plant immune system was stronger by mutants overexpressing swollenins than by knockouts and wild-type fungi [467].

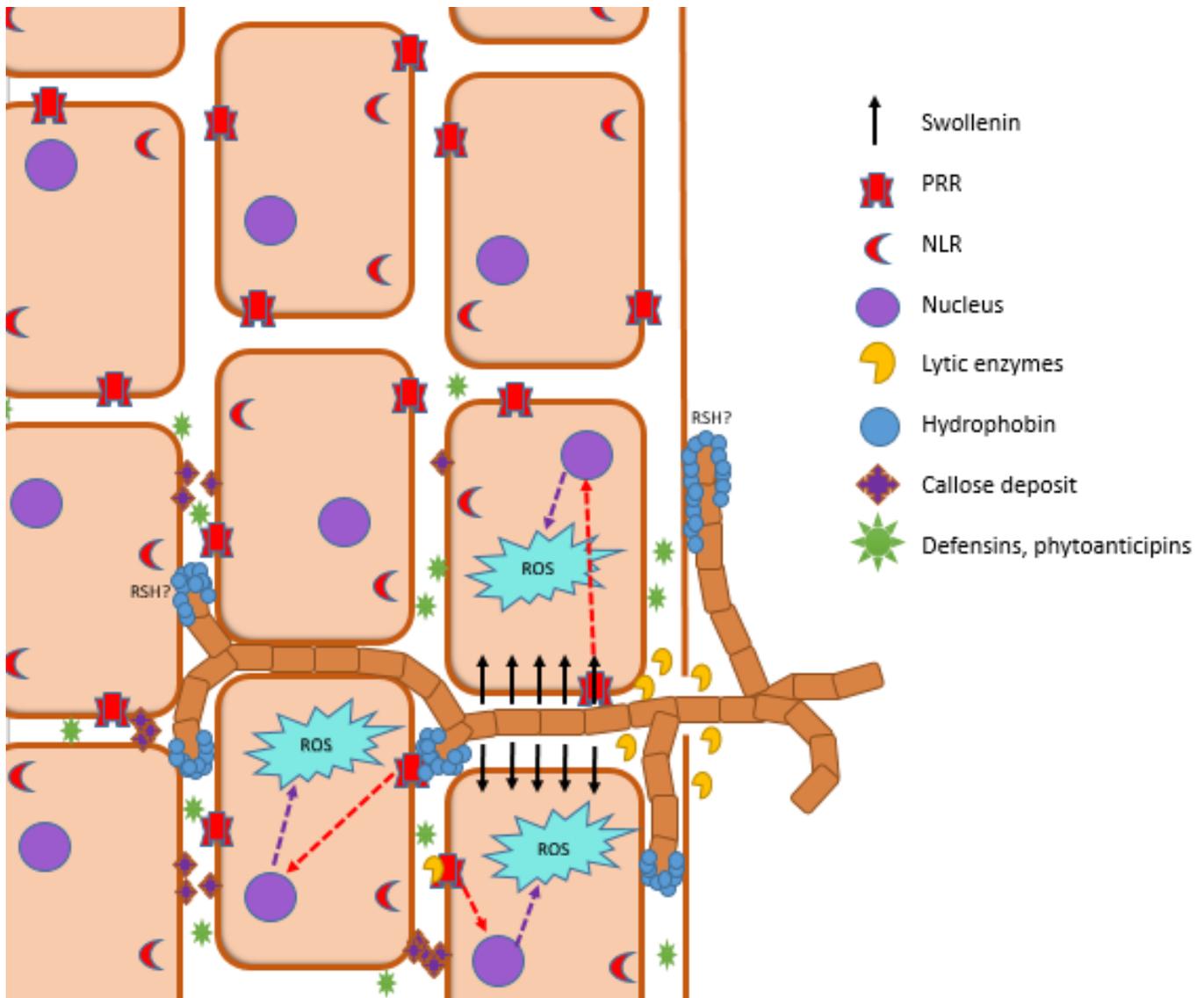


Figure 2. Colonization of root by a fungus belonging to *Trichoderma*. Adhesion and protection of hyphae are mediated by the layer of hydrophobins, whereas lytic enzymes enable penetration of the epidermis. Swollenins facilitate penetration of apoplast through an expansion-like effect on plant cell walls. Recognition of *Trichoderma*-derived MAMP molecules (swollenins, hydrophobins, cellulolytic enzymes, and chitin) triggers plant responses to infection, i.e., synthesis of antimicrobial compounds (defensins and phytoanticipins), synthesis of the callose wall in order to physically inhibit further penetration, and overproduction of ROS and possibly also alarmones. See text for more details.

Sucrose plays important role in plant colonization by *Trichoderma*. As demonstrated by Macías-Rodríguez et al. [468], the concentration of carbohydrates, mainly arabinose, xylose, myo-inositol, fructose, and glucose in root exudates of *L. esculentum* is higher before colonization by *T. atroviride*. Colonization of the root by *T. atroviride* changed the exudation pattern and sucrose became a major component of exudates. Root-derived sucrose specifically enables better growth of fungi belonging to *Trichoderma*, since AMF fungi prefer glucose and fructose as a source of carbon. Analysis of the proteome of maize

inoculated with *T. harzianum* T22 showed that 40 proteins involved in carbohydrate/starch metabolism were upregulated and 13 proteins were downregulated, which suggests that *T. harzianum* is able to modulate carbohydrate metabolism in colonized roots [413]. *T. virescens* was shown to produce invertase that hydrolyses plant-derived sucrose. The sucrolytic activity of fungal cells is crucial for root colonization but also to increase the photosynthetic rate in maize leaves [409].

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References

- Al-Ani, L.K.T. *Trichoderma*: Beneficial role in sustainable agriculture by plant disease management. In *Plant Microbiome: Stress Response*; Egamberdieva, D., Ahmad, P., Eds.; Springer: Singapore, 2018; Volume 5, pp. 105–126.
- Weltje, L.; Simpson, P.; Gross, M.; Crane, M.; Wheeler, J.R. Comparative acute and chronic sensitivity of fish and amphibians: A critical review of data. *Environ. Toxicol. Chem.* **2013**, *32*, 984–994. [[CrossRef](#)]
- Mukherjee, R.K.; Kumar, V.; Roy, K. Chemometric modeling of plant protection products (PPPs) for the prediction of acute contact toxicity against honey bees (*A. mellifera*): A 2D-QSAR approach. *J. Hazard. Mater.* **2022**, *423*, 127230. [[CrossRef](#)]
- Bruni, I.; Gentili, R.; de Mattia, F.; Cortis, P.; Rossi, G.; Labra, M. A multi-level analysis to evaluate the extinction risk of and conservation strategy for the aquatic fern *Marsilea quadrifolia* L. in Europe. *Aquat. Bot.* **2013**, *111*, 35–42. [[CrossRef](#)]
- Matarczyk, J.A.; Willis, A.J.; Vranjic, J.A.; Ash, J.E. Herbicides, weeds and endangered species: Management of bitou bush (*Chrysanthemoides monilifera* ssp. rotundata) with glyphosate and impacts on the endangered shrub *Pimelea spicata*. *Biol. Conserv.* **2002**, *108*, 133–141.
- Bikrol, A.; Saxena, N.; Singh, K. Response of *Glycine max* in relation to nitrogen fixation as influenced by fungicide seed treatment. *Int. J. Biochem. Biotechnol.* **2020**, *9*, 1–5.
- Santos, M.S.; Rodrigues, T.F.; Ferreira, E.; Megias, M.; Nogueira, M.A.; Hungria, M. Method for recovering and counting viable cells from maize seeds inoculated with *Azospirillum brasilense*. *J. Pure Appl. Microbiol.* **2020**, *14*, 195–204. [[CrossRef](#)]
- Zilli, J.É.; Ribeiro, K.G.; Campo, R.J.; Hungria, M. Influence of fungicide seed treatment on soybean nodulation and grain yield. *Rev. Bras. Cienc. Solo* **2009**, *33*, 917–923. [[CrossRef](#)]
- Streletskii, R.; Astaykina, A.; Krasnov, G.; Gorbatov, V. Changes in bacterial and fungal community of soil under treatment of pesticides. *Agronomy* **2022**, *12*, 124. [[CrossRef](#)]
- Santoyo, G.; Guzmán-Guzmán, P.; Parra-Cota, F.I.; de los Santos-Villalobos, S.; del Carmen Orozco-Mosqueda, M.; Glick, B.R. Plant growth stimulation by microbial consortia. *Agronomy* **2021**, *11*, 219. [[CrossRef](#)]
- Chaudhary, T.; Dixit, M.; Gera, R.; Shukla, A.K.; Prakash, A.; Gupta, G.; Shukla, P. Techniques for improving formulations of bioinoculants. *3 Biotech.* **2020**, *10*, 199. [[CrossRef](#)]
- Romano, I.; Ventrino, V.; Pepe, O. Effectiveness of plant beneficial microbes: Overview of the methodological approaches for the assessment of root colonization and persistence. *Front. Plant Sci.* **2020**, *11*, 6. [[CrossRef](#)]
- Maitra, S.; Brestic, M.; Bhadra, P.; Shankar, T.; Praharaj, S.; Palai, J.B.; Shah, M.M.R.; Barek, V.; Ondrisik, P.; Skalický, M.; et al. Bioinoculants-natural biological resources for sustainable plant production. *Microorganisms* **2022**, *10*, 51. [[CrossRef](#)]
- Basu, A.; Prasad, P.; Das, S.N.; Kalam, S.; Sayyed, R.Z.; Reddy, M.S.; Enshasy, H. Plant growth promoting rhizobacteria (PGPR) as green bioinoculants: Recent developments, constraints, and prospects. *Sustainability* **2021**, *13*, 1140. [[CrossRef](#)]
- Martínez-Hidalgo, P.; Maymon, M.; Pule-Meulenberg, F.; Hirsch, A.M. Engineering root microbiomes for healthier crops and soils using beneficial, environmentally safe bacteria. *Can. J. Microbiol.* **2019**, *65*, 91–104. [[CrossRef](#)]
- Cai, F.; Chen, W.; Wei, Z.; Pang, G.; Li, R.; Ran, W.; Shen, Q. Colonization of *Trichoderma harzianum* strain SQR-T037 on tomato roots and its relationship to plant growth, nutrient availability and soil microflora. *Plant Soil* **2015**, *388*, 337–350. [[CrossRef](#)]
- Rojas-Tapias, D.F.; Bonilla, R.; Dussán, J. Effect of inoculation and co-inoculation of *Acinetobacter* sp. RG30 and *Pseudomonas putida* GN04 on growth, fitness, and copper accumulation of maize (*Zea mays*). *Water Air Soil Pollut.* **2014**, *225*, 2232. [[CrossRef](#)]
- Patel, P.; Gajjar, H.; Joshi, B.; Krishnamurthy, R.; Amaresan, N. Inoculation of salt-tolerant *Acinetobacter* sp. (RSC9) improves the sugarcane (*Saccharum* sp. hybrids) growth under salinity stress condition. *Sugar Tech* **2022**, *24*, 494–501. [[CrossRef](#)]
- Chihaoui, S.A.; Trabelsi, D.; Jdey, A.; Mhadhbi, H.; Mhamdi, R. Inoculation of *Phaseolus vulgaris* with the nodule-endophyte *Agrobacterium* sp. 10C2 affects richness and structure of rhizosphere bacterial communities and enhances nodulation and growth. *Arch. Microbiol.* **2015**, *197*, 805–813. [[CrossRef](#)]
- Sharma, M.; Mishra, V.; Rau, N.; Sharma, R.S. Increased iron-stress resilience of maize through inoculation of siderophore-producing *Arthrobacter globiformis* from mine. *J. Basic Microbiol.* **2016**, *56*, 719–735. [[CrossRef](#)]

21. Fan, P.; Chen, D.; He, Y.; Zhou, Q.; Tian, Y.; Gao, L. Alleviating salt stress in tomato seedlings using *Arthrobacter* and *Bacillus megaterium* isolated from the rhizosphere of wild plants grown on saline–alkaline lands. *Int. J. Phytoremediation* **2016**, *18*, 1113–1121. [[CrossRef](#)]
22. Parmasi, Z.; Tahmasebi, Z.; Zare, M.J.; Nourollahi, K.; Kanouni, H. Biocontrol of Ascochyta blight by *Azospirillum* sp. depending on the degree of resistance of chickpea genotypes. *J. Phytopathol.* **2019**, *167*, 601–607. [[CrossRef](#)]
23. Mazhar, R.; Ilyas, N.; Saeed, M.; Bibi, F.; Batool, N. Biocontrol and salinity tolerance potential of *Azospirillum lipoferum* and its inoculation effect in wheat crop. *Int. J. Agric. Biol.* **2015**, *18*, 494–500. [[CrossRef](#)]
24. Shirinbayan, S.; Khosravi, H.; Malakouti, M.J. Alleviation of drought stress in maize (*Zea mays*) by inoculation with *Azotobacter* strains isolated from semi-arid regions. *Appl. Soil Ecol.* **2019**, *133*, 138–145. [[CrossRef](#)]
25. Chen, L.; Liu, Y.; Wu, G.; Njeri, K.V.; Shen, Q.; Zhang, N.; Zhang, R. Induced maize salt tolerance by rhizosphere inoculation of *Bacillus amyloliquefaciens* SQR9. *Physiol. Plant.* **2016**, *158*, 34–44. [[CrossRef](#)]
26. Hafeez, F.Y.; Safdar, M.E.; Chaudhry, A.U.; Malik, K.A. Rhizobial inoculation improves seedling emergence, nutrient uptake and growth of cotton. *Aust. J. Exp. Agric.* **2004**, *44*, 617–622. [[CrossRef](#)]
27. Naveed, M.; Hussain, M.B.; Zahir, Z.A.; Mitter, B.; Sessitsch, A. Drought stress amelioration in wheat through inoculation with *Burkholderia phytofirmans* strain PsJN. *Plant Growth Regul.* **2014**, *73*, 121–131. [[CrossRef](#)]
28. Bernabeu, P.R.; Pistorio, M.; Torres-Tejerizo, G.; Estrada-De los Santos, P.; Galar, M.L.; Boiardi, J.L.; Luna, M.F. Colonization and plant growth-promotion of tomato by *Burkholderia tropica*. *Sci. Hortic.* **2015**, *191*, 113–120. [[CrossRef](#)]
29. Tsuda, K.; Kosaka, Y.; Tsuge, S.; Kub, Y.; Horin, O. Evaluation of the endophyte *Enterobacter cloacae* SM10 isolated from spinach roots for biological control against *Fusarium* wilt of spinach. *J. Gen. Plant Pathol.* **2001**, *67*, 78–84. [[CrossRef](#)]
30. Ngom, M.; Gray, K.; Diagne, N.; Oshone, R.; Fardoux, J.; Gherbi, H.; Hocher, V.; Svistoonoff, S.; Laplaze, L.; Tisa, L.S.; et al. Symbiotic performance of diverse *Frankia* strains on salt-stressed *Casuarina glauca* and *Casuarina equisetifolia* plants. *Front. Plant Sci.* **2016**, *7*, 1331. [[CrossRef](#)]
31. Grossi, C.E.M.; Fantino, E.; Serral, F.; Zawoznik, M.S.; Fernandez Do Porto, D.A.; Ulloa, R.M. *Methylobacterium* sp. 2A is a plant growth-promoting rhizobacteria that has the potential to improve potato crop yield under adverse conditions. *Front. Plant Sci.* **2020**, *11*, 71. [[CrossRef](#)]
32. Hernández-Montiel, L.G.; Chiquito-Contreras, C.J.; Murillo-Amador, B.; Vidal-Hernández, L.; Quiñones-Aguilar, E.E.; Chiquito-Contreras, R.G. Efficiency of two inoculation methods of *Pseudomonas putida* on growth and yield of tomato plants. *J. Soil Sci. Plant Nutr.* **2017**, *17*, 1003–1012. [[CrossRef](#)]
33. Fu, Q.; Liu, C.; Ding, N.; Lin, Y.; Guo, B. Ameliorative effects of inoculation with the plant growth-promoting rhizobacterium *Pseudomonas* sp. DW1 on growth of eggplant (*Solanum melongena* L.) seedlings under salt stress. *Agric. Water Manag.* **2010**, *97*, 1994–2000. [[CrossRef](#)]
34. Szymańska, S.; Dąbrowska, G.B.; Tyburski, J.; Niedojadło, K.; Piernik, A.; Hryniewicz, K. Boosting the *Brassica napus* L. tolerance to salinity by the halotolerant strain *Pseudomonas stutzeri* ISE12. *Environ. Exp. Bot.* **2019**, *163*, 55–68. [[CrossRef](#)]
35. Biswas, J.C.; Ladha, J.K.; Dazzo, F.B. Rhizobia inoculation improves nutrient uptake and growth of lowland rice. *Soil Sci. Soc. Am. J.* **2000**, *64*, 1644–1650. [[CrossRef](#)]
36. Biswas, J.C.; Ladha, J.K.; Dazzo, F.B.; Yanni, Y.G.; Rolfe, B.G. Rhizobial inoculation influences seedling vigor and yield of rice. *Agron. J.* **2000**, *92*, 880–886. [[CrossRef](#)]
37. Turhan, E.; Kiran, S.; Ates, Ç.; Ates, O.; Kusvuran, S.; Ellialtioglu, S.S. Ameliorative effects of inoculation with *Serratia marcescens* and grafting on growth of eggplant seedlings under salt stress. *J. Plant Nutr.* **2020**, *43*, 594–603. [[CrossRef](#)]
38. Palaniyandi, S.A.; Damodharan, K.; Yang, S.H.; Suh, J.W. *Streptomyces* sp. strain PGPA39 alleviates salt stress and promotes growth of ‘Micro Tom’ tomato plants. *J. Appl. Microbiol.* **2014**, *117*, 766–773. [[CrossRef](#)]
39. Samac, D.A.; Kinkel, L.L. Suppression of the root-lesion nematode (*Pratylenchus penetrans*) in alfalfa (*Medicago sativa*) by *Streptomyces* spp. *Plant Soil* **2001**, *235*, 35–44. [[CrossRef](#)]
40. Mauricio-Castillo, J.A.; Salas-Muñoz, S.; Reveles-Torres, L.R.; Salas-Luevano, M.A.; Salazar-Badillo, F.B. Could *Alternaria solani* IA300 be a plant growth-promoting fungus? *Eur. J. Plant Pathol.* **2020**, *157*, 413–419. [[CrossRef](#)]
41. Galeano, R.M.S.; Franco, D.G.; Chaves, P.O.; Giannesi, G.C.; Masui, D.C.; Ruller, R.; Corrêa, B.O.; da Silva Brasil, M.; Zanoelo, F.F. Plant growth promoting potential of endophytic *Aspergillus niger* 9-p isolated from native forage grass in Pantanal of Nhecolândia region, Brazil. *Rhizosphere* **2021**, *18*, 100332. [[CrossRef](#)]
42. Khan, A.L.; Hamayun, M.; Kim, Y.H.; Kang, S.M.; Lee, J.H.; Lee, I.J. Gibberellins producing endophytic *Aspergillus fumigatus* sp. LH02 influenced endogenous phytohormonal levels, isoflavonoids production and plant growth in salinity stress. *Process Biochem.* **2011**, *46*, 440–447. [[CrossRef](#)]
43. Dąbrowska, G.B.; Garstecka, Z.; Trejgell, A.; Dąbrowski, H.P.; Konieczna, W.; Szymp-Borowska, I. The impact of forest fungi on promoting growth and development of *Brassica napus* L. *Agronomy* **2021**, *11*, 2475. [[CrossRef](#)]
44. Velásquez, A.; Vega-Celedón, P.; Fiaschi, G.; Agnolucci, M.; Avio, L.; Giovannetti, M.; D’Onofrio, C.; Seeger, M. Responses of *Vitis vinifera* cv. Cabernet Sauvignon roots to the arbuscular mycorrhizal fungus *Funneliformis mosseae* and the plant growth-promoting rhizobacterium *Ensifer meliloti* include changes in volatile organic compounds. *Mycorrhiza* **2020**, *30*, 161–170. [[CrossRef](#)]
45. Saldajeno, M.G.B.; Hyakumachi, M. The plant growth-promoting fungus *Fusarium equiseti* and the arbuscular mycorrhizal fungus *Glomus mosseae* stimulate plant growth and reduce severity of anthracnose and damping-off diseases in cucumber (*Cucumis sativus*) seedlings. *Ann. Appl. Biol.* **2011**, *159*, 28–40. [[CrossRef](#)]

46. Radhakrishnan, R.; Khan, A.L.; Kang, S.M.; Lee, I.J. A comparative study of phosphate solubilization and the host plant growth promotion ability of *Fusarium verticillioides* RK01 and *Humicola* sp. KNU01 under salt stress. *Ann. Microbiol.* **2015**, *65*, 585–593. [[CrossRef](#)]
47. Estaún, V.; Camprubí, A.; Calvet, C.; Pinochet, J. Nursery and field response of olive trees inoculated with two arbuscular mycorrhizal fungi, *Glomus intraradices* and *Glomus mosseae*. *J. Am. Soc. Hortic. Sci.* **2003**, *128*, 767–775. [[CrossRef](#)]
48. Senthil Kumar, C.M.; Jacob, T.K.; Devasahayam, S.; Thomas, S.; Geethu, C. Multifarious plant growth promotion by an entomopathogenic fungus *Lecanicillium psalliota*. *Microbiol. Res.* **2018**, *207*, 153–160. [[CrossRef](#)]
49. Ozimek, E.; Jaroszuk-Ścisiel, J.; Bohacz, J.; Kornilłowicz-Kowalska, T.; Tyśkiewicz, R.; Słomka, A.; Nowak, A.; Hanaka, A. Synthesis of indoleacetic acid, gibberellic acid and ACC-deaminase by *Mortierella* strains promote winter wheat seedlings growth under different conditions. *Int. J. Mol. Sci.* **2018**, *19*, 3218. [[CrossRef](#)]
50. Rozpądek, P.; Domka, A.; Ważny, R.; Nosek, M.; Jędrzejczyk, R.; Tokarz, K.; Turnau, K. How does the endophytic fungus *Mucor* sp. improve *Arabidopsis arenosa* vegetation in the degraded environment of a mine dump? *Environ. Exp. Bot.* **2018**, *147*, 31–42. [[CrossRef](#)]
51. Vessey, J.K.; Heisinger, K.G. Effect of *Penicillium bilaii* inoculation and phosphorus fertilisation on root and shoot parameters of field-grown pea. *Can. J. Microbiol.* **2011**, *81*, 361–366. [[CrossRef](#)]
52. Wakelin, S.A.; Gupta, V.V.S.R.; Harvey, P.R.; Ryder, M.H. The effect of *Penicillium* fungi on plant growth and phosphorus mobilization in neutral to alkaline soils from southern Australia. *Can. J. Microbiol.* **2007**, *53*, 106–115. [[CrossRef](#)]
53. Elsharkawy, M.M. Induced systemic resistance against Cucumber mosaic virus by *Phoma* sp. GS8-2 stimulates transcription of pathogenesis-related genes in *Arabidopsis*. *Pest. Manag. Sci.* **2019**, *75*, 859–866. [[CrossRef](#)]
54. Elsharkawy, M.M.; El-Khateeb, N.M.M. Antifungal activity and resistance induction against *Sclerotium cepivorum* by plant growth-promoting fungi in onion plants. *Egypt. J. Biol. Pest Control* **2019**, *29*, 68. [[CrossRef](#)]
55. Baron, N.C.; de Souza Pollo, A.; Rigobelo, E.C. *Purpureocillium lilacinum* and *Metarhizium marquandii* as plant growth-promoting fungi. *PeerJ* **2020**, *2020*, e9005. [[CrossRef](#)]
56. Janowska, B.; Andrzejak, R.; Kosiada, T. The influence of fungi of the *Trichoderma* genus on the flowering of *Freesia refracta* Klatt ‘Argentea’ in winter. *Hortic. Sci.* **2020**, *47*, 203–210. [[CrossRef](#)]
57. Vinayarani, G.; Prakash, H.S. Fungal endophytes of turmeric (*Curcuma longa* L.) and their biocontrol potential against pathogens *Pythium aphanidermatum* and *Rhizoctonia solani*. *World J. Microbiol. Biotechnol.* **2018**, *34*, 49. [[CrossRef](#)]
58. Nuangmek, W.; Aiduang, W.; Kumla, J.; Lumyong, S.; Suwannarach, N. Evaluation of a newly identified endophytic fungus, *Trichoderma phayaoense* for plant growth promotion and biological control of gummy stem blight and wilt of muskmelon. *Front. Microbiol.* **2021**, *12*, 410. [[CrossRef](#)]
59. Znajewska, Z.; Dąbrowska, G.; Narbutt, O. *Trichoderma viride* strains stimulating the growth and development of winter rapeseed (*Brassica napus* L.). *Prog. Plant Prot.* **2018**, *58*, 264–269.
60. Singh, D.P.; Prabha, R.; Yandigeri, M.S.; Arora, D.K. Cyanobacteria-mediated phenylpropanoids and phytohormones in rice (*Oryza sativa*) enhance plant growth and stress tolerance. *Anton. Leeuw. Int. J.* **2011**, *100*, 557–568. [[CrossRef](#)]
61. Prasanna, R.; Chaudhary, V.; Gupta, V.; Babu, S.; Kumar, A.; Singh, R.; Shivay, Y.S.; Nain, L. Cyanobacteria mediated plant growth promotion and bioprotection against *Fusarium* wilt in tomato. *Eur. J. Plant Pathol.* **2013**, *136*, 337–353. [[CrossRef](#)]
62. Priya, H.; Prasanna, R.; Ramakrishnan, B.; Bidiyaran, N.; Babu, S.; Thapa, S.; Renuka, N. Influence of cyanobacterial inoculation on the culturable microbiome and growth of rice. *Microbiol. Res.* **2015**, *171*, 78–89. [[CrossRef](#)]
63. Babu, S.; Prasanna, R.; Bidiyaran, N.; Singh, R. Analysing the colonisation of inoculated cyanobacteria in wheat plants using biochemical and molecular tools. *J. Appl. Phycol.* **2015**, *27*, 327–338. [[CrossRef](#)]
64. Kim, S.J.; Ko, E.J.; Hong, J.K.; Jeun, Y.C. Ultrastructures of *Colletotrichum orbiculare* in cucumber leaves expressing systemic acquired resistance mediated by *Chlorella fusca*. *Plant Pathol. J.* **2018**, *34*, 113. [[CrossRef](#)]
65. Mohamed Taha, T.; Youssef, M.A. Improvement of growth parameters of *Zea mays* and properties of soil inoculated with two *Chlorella* species. *Rep. Opin.* **2015**, *7*, 22–27.
66. Agwa, O.K.; Ogugbue, C.J.; Williams, E.E. Growth promotion of *Telfairia occidentalis* by application of *Chlorella vulgaris* (bioinoculant) colonized seeds and soil under tropical field conditions. *Am. J. Plant Sci.* **2018**, *9*, 403–415. [[CrossRef](#)]
67. Kuang, X.; Gu, J.D.; Tie, B.Q.; Yao, B.; Shao, J. Interactive effects of cadmium and *Microcystis aeruginosa* (cyanobacterium) on the growth, antioxidative responses and accumulation of cadmium and microcystins in rice seedlings. *Ecotoxicology* **2016**, *25*, 1588–1599. [[CrossRef](#)]
68. Hussain, A.; Hamayun, M.; Shah, S.T. Root colonization and phyto-stimulation by phytohormones producing entophytic *Nostoc* sp. AH-12. *Curr. Microbiol.* **2013**, *67*, 624–630. [[CrossRef](#)]
69. Maqubela, M.P.; Mkeni, P.N.S.; Issa, O.M.; Pardo, M.T.; D’Acqui, L.P. *Nostoc* cyanobacterial inoculation in South African agricultural soils enhances soil structure, fertility, and maize growth. *Plant Soil* **2009**, *315*, 79–92. [[CrossRef](#)]
70. Barone, V.; Puglisi, I.; Fragalà, F.; lo Piero, A.R.; Giuffrida, F.; Baglieri, A. Novel bioprocess for the cultivation of microalgae in hydroponic growing system of tomato plants. *J. Appl. Phycol.* **2019**, *31*, 465–470. [[CrossRef](#)]
71. Seifikalhor, M.; Hassani, S.B.; Aliniaiefard, S. Seed priming by cyanobacteria (*Spirulina platensis*) and salep gum enhances tolerance of maize plant against cadmium toxicity. *J. Plant Growth Regul.* **2020**, *39*, 1009–1021. [[CrossRef](#)]
72. Rana, A.; Joshi, M.; Prasanna, R.; Shivay, Y.S.; Nain, L. Biofortification of wheat through inoculation of plant growth promoting rhizobacteria and cyanobacteria. *Eur. J. Soil Biol.* **2012**, *50*, 118–126. [[CrossRef](#)]

73. Flores, A.C.; Luna, A.A.E.; Portugal, V.O. Yield and quality enhancement of marigold flowers by inoculation with *Bacillus subtilis* and *Glomus fasciculatum*. *J. Sustain. Agric.* **2007**, *31*, 21–31. [[CrossRef](#)]
74. Nacoon, S.; Jogloy, S.; Riddech, N.; Mongkolthananuk, W.; Kuyper, T.W.; Boonlue, S. Interaction between phosphate solubilizing bacteria and arbuscular mycorrhizal fungi on growth promotion and tuber inulin content of *Helianthus tuberosus* L. *Sci. Rep.* **2020**, *10*, 4916. [[CrossRef](#)]
75. Oliveira, R.S.; Carvalho, P.; Marques, G.; Ferreira, L.; Nunes, M.; Rocha, I.; Ma, Y.; Carvalho, M.F.; Vosátka, M.; Freitas, H. Increased protein content of chickpea (*Cicer arietinum* L.) inoculated with arbuscular mycorrhizal fungi and nitrogen-fixing bacteria under water deficit conditions. *J. Sci. Food Agric.* **2017**, *97*, 4379–4385. [[CrossRef](#)]
76. Bona, E.; Cantamessa, S.; Massa, N.; Manassero, P.; Marsano, F.; Copetta, A.; Lingua, G.; D'Agostino, G.; Gamalero, E.; Berta, G. Arbuscular mycorrhizal fungi and plant growth-promoting pseudomonads improve yield, quality and nutritional value of tomato: A field study. *Mycorrhiza* **2017**, *27*, 1–11. [[CrossRef](#)]
77. Hidri, R.; Barea, J.M.; Mahmoud, O.M.B.; Abdelly, C.; Azcón, R. Impact of microbial inoculation on biomass accumulation by *Sulla carnosa* provenances, and in regulating nutrition, physiological and antioxidant activities of this species under non-saline and saline conditions. *J. Plant Physiol.* **2016**, *201*, 28–41. [[CrossRef](#)]
78. Armada, E.; Probanza, A.; Roldán, A.; Azcón, R. Native plant growth promoting bacteria *Bacillus thuringiensis* and mixed or individual mycorrhizal species improved drought tolerance and oxidative metabolism in *Lavandula dentata* plants. *J. Plant Physiol.* **2016**, *192*, 1–12. [[CrossRef](#)]
79. Duc, N.H.; Mayer, Z.; Pék, Z.; Helyes, L.; Posta, K. Combined inoculation of arbuscular mycorrhizal fungi, *Pseudomonas fluorescens* and *Trichoderma* spp. for enhancing defense enzymes and yield of three pepper cultivars. *Appl. Ecol. Environ. Res.* **2017**, *15*, 1815–1829. [[CrossRef](#)]
80. Pandey, A.; Yarzabal, L.A. Bioprospecting cold-adapted plant growth promoting microorganisms from mountain environments. *Appl. Microbiol. Biotechnol.* **2019**, *103*, 643–657. [[CrossRef](#)]
81. Van Elsas, J.D.; Chiurazzi, M.; Mallon, C.A.; Elhottová, D.; Křišťůfek, V.; Salles, J.F. Microbial diversity determines the invasion of soil by a bacterial pathogen. *PNAS* **2012**, *109*, 1159–1164. [[CrossRef](#)]
82. Goswami, D.; Thakker, J.N.; Dhandhukia, P.C. Portraying mechanics of plant growth promoting rhizobacteria (PGPR): A review. *Cogent. Food Agric.* **2016**, *2*, 1127500. [[CrossRef](#)]
83. Middleton, H.; Yergeau, É.; Monard, C.; Combier, J.-P.; el Amrani, A. Rhizospheric plant–microbe interactions: miRNAs as a key mediator. *Trends Plant Sci.* **2021**, *26*, 132–141. [[CrossRef](#)] [[PubMed](#)]
84. Manfredini, A.; Malusà, E.; Costa, C.; Pallottino, F.; Mocali, S.; Pinzari, F.; Canfora, L. Current methods, common practices, and perspectives in tracking and monitoring bioinoculants in soil. *Front. Microbiol.* **2021**, *12*, 698491. [[CrossRef](#)] [[PubMed](#)]
85. Shivanna, M.B.; Meera, M.S.; Hyakumachi, M. Sterile fungi from zoysiagrass rhizosphere as plant growth promoters in spring wheat. *Can. J. Microbiol.* **1994**, *40*, 637–644. [[CrossRef](#)]
86. Dąbrowska, G.; Hryniewicz, K.; Mierek-Adamska, A.; Goc, A. The sensitivity of spring and winter varieties of oilseed rape to heavy metals and rhizobacteria. *Oilseed Crop.* **2012**, *33*, 201–220.
87. Gnanamanickam, S.S.; Immanuel, J.E. Epiphytic bacteria, their ecology and functions. In *Plant-Associated Bacteria*; Gnanamanickam, S.S., Ed.; Springer: Dordrecht, The Netherlands, 2006; pp. 131–153.
88. Kucharska, K.; Wachowska, U. The microbiome on the leaves of crop plants. *Adv. Microbiol.* **2014**, *53*, 352–359.
89. Martins, G.; Lauga, B.; Miot-Sertier, C.; Mercier, A.; Lonvaud, A.; Soulas, M.-L.; Soulas, G.; Masneuf-Pomarède, I. Characterization of epiphytic bacterial communities from grapes, leaves, bark and soil of grapevine plants grown, and their relations. *PLoS ONE* **2013**, *8*, e73013. [[CrossRef](#)]
90. Whipps, J.M. Microbial interactions and biocontrol in the rhizosphere. *J. Exp. Bot.* **2001**, *52*, 487–511. [[CrossRef](#)]
91. Gong, T.; Xin, X. Phyllosphere microbiota: Community dynamics and its interaction with plant hosts. *J. Integr. Plant Biol.* **2021**, *63*, 297–304. [[CrossRef](#)]
92. Contreras-Cornejo, H.A.; Macías-Rodríguez, L.; Cortés-Penagos, C.; López-Bucio, J. *Trichoderma virens*, a plant beneficial fungus, enhances biomass production and promotes lateral root growth through an auxin-dependent mechanism in *Arabidopsis*. *Plant Physiol.* **2009**, *149*, 1579–1592. [[CrossRef](#)]
93. You, Y.-H.; Yoon, H.; Kang, S.-M.; Shin, J.-H.; Choo, Y.-S.; Lee, I.-J.; Lee, J.-M.; Kim, J.-G. Fungal diversity and plant growth promotion of endophytic fungi from six halophytes in Suncheon Bay. *J. Microbiol. Biotechnol.* **2012**, *22*, 1549–1556. [[CrossRef](#)] [[PubMed](#)]
94. Bergottini, V.M.; Otegui, M.B.; Sosa, D.A.; Zapata, P.D.; Mulot, M.; Rebord, M.; Zopfi, J.; Wiss, F.; Benrey, B.; Junier, P. Bioinoculation of yerba mate seedlings (*Ilex paraguariensis* St. Hill.) with native plant growth-promoting rhizobacteria: A sustainable alternative to improve crop yield. *Biol. Fertil. Soils* **2015**, *51*, 749–755. [[CrossRef](#)]
95. Poonguzhali, S.; Madhaiyan, M.; Sa, T. Isolation and identification of phosphate solubilizing bacteria from chinese cabbage and their effect on growth and phosphorus utilization of plants. *J. Microbiol. Biotechnol.* **2008**, *18*, 773–777. [[PubMed](#)]
96. Zhang, C.; Kong, F. Isolation and identification of potassium-solubilizing bacteria from tobacco rhizospheric soil and their effect on tobacco plants. *Appl. Soil Ecol.* **2014**, *82*, 18–25. [[CrossRef](#)]
97. Reed, M.L.E.; Glick, B.R. Growth of canola (*Brassica napus*) in the presence of plant growth-promoting bacteria and either copper or polycyclic aromatic hydrocarbons. *Can. J. Microbiol.* **2005**, *51*, 1061–1069. [[CrossRef](#)]

98. Jousset, A.; Rochat, L.; Lanoue, A.; Bonkowski, M.; Keel, C.; Scheu, S. Plants respond to pathogen infection by enhancing the antifungal gene expression of root-associated bacteria. *Mol. Plant-Microbe Interact.* **2011**, *24*, 352–358. [[CrossRef](#)]
99. Schirmböck, M.; Lorito, M.; Wang, Y.L.; Hayes, C.K.; Arisan-Atac, I.; Scala, F.; Harman, G.E.; Kubicek, C.P. Parallel formation and synergism of hydrolytic enzymes and peptaibol antibiotics, molecular mechanisms involved in the antagonistic action of *Trichoderma harzianum* against phytopathogenic fungi. *Appl. Environ. Microbiol.* **1994**, *60*, 4364–4370. [[CrossRef](#)]
100. Crowley, D.E. Microbial siderophores in the plant rhizosphere. In *Iron Nutrition in Plants and Rhizospheric Microorganisms*; Barton, L.L., Abadia, J., Eds.; Springer: Dordrecht, The Netherlands, 2006; pp. 169–198.
101. Pinedo, I.; Ledger, T.; Greve, M.; Poupin, M.J. *Burkholderia phytofirmans* PsJN induces long-term metabolic and transcriptional changes involved in *Arabidopsis thaliana* salt tolerance. *Front. Plant Sci.* **2015**, *6*, 466. [[CrossRef](#)]
102. Coppola, M.; Cascone, P.; di Lelio, I.; Woo, S.L.; Lorito, M.; Rao, R.; Pennacchio, F.; Guerrieri, E.; Digilio, M.C. *Trichoderma atroviride* P1 colonization of tomato plants enhances both direct and indirect defense barriers against insects. *Front. Physiol.* **2019**, *10*, 813. [[CrossRef](#)]
103. Ardanov, P.; Lyastchenko, S.; Karppinen, K.; Häggman, H.; Kozyrovska, N.; Pirttilä, A.M. Effects of *Methylobacterium* sp. on emergence, yield, and disease prevalence in three cultivars of potato (*Solanum tuberosum* L.) were associated with the shift in endophytic microbial community. *Plant Soil* **2016**, *405*, 299–310. [[CrossRef](#)]
104. Lynch, J.M.; Leij, F. Rhizosphere. In *eLS.*; John Wiley & Sons: Hoboken, NJ, USA, 2012.
105. Kawasaki, A.; Donn, S.; Ryan, P.R.; Mathesius, U.; Devilla, R.; Jones, A.; Watt, M. Microbiome and exudates of the root and rhizosphere of *Brachypodium distachyon*, a model for wheat. *PLoS ONE* **2016**, *11*, e0164533. [[CrossRef](#)] [[PubMed](#)]
106. Li, X.G.; Zhang, T.L.; Wang, X.X.; Hua, K.; Zhao, L.; Han, Z.M. The composition of root exudates from two different resistant peanut cultivars and their effects on the growth of soil-borne pathogen. *Int. J. Biol. Sci.* **2013**, *9*, 164. [[CrossRef](#)] [[PubMed](#)]
107. Lucas García, J.A.; Barbas, C.; Probanza, A.; Barrientos, M.L.; Gutierrez Mañero, F.J. Low molecular weight organic acids and fatty acids in root exudates of two *Lupinus* cultivars at flowering and fruiting stages. *Phytochem. Anal.* **2001**, *12*, 305–311. [[CrossRef](#)]
108. Narasimhan, K.; Basheer, C.; Bajic, V.B.; Swarup, S. Enhancement of plant-microbe interactions using a rhizosphere metabolomics-driven approach and its application in the removal of polychlorinated biphenyls. *Plant Physiol.* **2003**, *132*, 146–153. [[CrossRef](#)] [[PubMed](#)]
109. Nóbrega, F.M.; Santos, I.S.; da Cunha, M.; Carvalho, A.O.; Gomes, V.M. Antimicrobial proteins from cowpea root exudates: Inhibitory activity against *Fusarium oxysporum* and purification of a chitinase-like protein. *Plant Soil* **2005**, *272*, 223–232. [[CrossRef](#)]
110. Schönwitz, R.; Ziegler, H. Exudation of water-soluble vitamins and of some carbohydrates by intact roots of maize seedlings (*Zea mays* L.) into a mineral nutrient solution. *Z. Pflanzenphysiol.* **1982**, *107*, 7–14. [[CrossRef](#)]
111. Wang, J.; Ding, Z.; Bian, J.; Bo, T.; Liu, Y. Chemotaxis response of *Meloidogyne incognita* to volatiles and organic acids from root exudates. *Rhizosphere* **2021**, *17*, 100320. [[CrossRef](#)]
112. Williams, A.; Langridge, H.; Straathof, A.L.; Muhamadali, H.; Hollywood, K.A.; Goodacre, R.; de Vries, F.T. Root functional traits explain root exudation rate and composition across a range of grassland species. *J. Ecol.* **2022**, *110*, 21–33. [[CrossRef](#)]
113. Aulakh, M.S.; Wassmann, R.; Bueno, C.; Kreuzwieser, J.; Rennenberg, H. Characterization of root exudates at different growth stages of ten rice (*Oryza sativa* L.) cultivars. *Plant Biol.* **2001**, *3*, 139–148. [[CrossRef](#)]
114. Bekkara, F.; Jay, M.; Viricel, M.R.; Rome, S. Distribution of phenolic compounds within seed and seedlings of two *Vicia faba* cvs differing in their seed tannin content, and study of their seed and root phenolic exudations. *Plant Soil* **1998**, *203*, 27–36. [[CrossRef](#)]
115. Watt, M.; Evans, J.R. Linking development and determinacy with organic acid efflux from proteoid roots of white lupin grown with low phosphorus and ambient or elevated atmospheric CO₂ concentration. *Plant Physiol.* **1999**, *120*, 705–716. [[CrossRef](#)] [[PubMed](#)]
116. Tawaraya, K.; Horie, R.; Saito, A.; Shinano, T.; Wagatsuma, T.; Saito, K.; Oikawa, A. Metabolite profiling of shoot extracts, root extracts, and root exudates of rice plant under phosphorus deficiency. *J. Plant Nutr.* **2013**, *36*, 1138–1159. [[CrossRef](#)]
117. Tawaraya, K.; Horie, R.; Shinano, T.; Wagatsuma, T.; Saito, K.; Oikawa, A. Metabolite profiling of soybean root exudates under phosphorus deficiency. *Soil Sci. Plant Nutr.* **2014**, *60*, 679–694. [[CrossRef](#)]
118. Neumann, G.; Römheld, V. Root excretion of carboxylic acids and protons in phosphorus-deficient plants. *Plant Soil* **1999**, *211*, 121–130. [[CrossRef](#)]
119. Carvalhais, L.C.; Dennis, P.G.; Fedoseyenko, D.; Hajirezaei, M.R.; Borriss, R.; von Wirén, N. Root exudation of sugars, amino acids, and organic acids by maize as affected by nitrogen, phosphorus, potassium, and iron deficiency. *J. Plant Nutr. Soil Sci.* **2011**, *174*, 3–11. [[CrossRef](#)]
120. Gargallo-Garriga, A.; Preece, C.; Sardans, J.; Oravec, M.; Urban, O.; Peñuelas, J. Root exudate metabolomes change under drought and show limited capacity for recovery. *Sci. Rep.* **2018**, *8*, 12696. [[CrossRef](#)]
121. Henry, A.; Doucette, W.; Norton, J.; Bugbee, B. Changes in crested wheatgrass root exudation caused by flood, drought, and nutrient stress. *J. Environ. Qual.* **2007**, *36*, 904–912. [[CrossRef](#)]
122. Wang, E.L.H.; Bergeson, G.B. Biochemical changes in root exudate and xylem sap of tomato plants infected with *Meloidogyne incognita*. *J. Nematol.* **1974**, *6*, 194.
123. Neumann, G.; Bott, S.; Ohler, M.A.; Mock, H.P.; Lippmann, R.; Grosch, R.; Smalla, K. Root exudation and root development of lettuce (*Lactuca sativa* L. Cv. Tizian) as affected by different soils. *Front. Microbiol.* **2014**, *5*, 2. [[CrossRef](#)]
124. Guttman, D.S.; McHardy, A.C.; Schulze-Lefert, P. Microbial genome-enabled insights into plant-microorganism interactions. *Nat. Rev. Genet.* **2014**, *15*, 797–813. [[CrossRef](#)]

125. Mohanram, S.; Kumar, P. Rhizosphere microbiome: Revisiting the synergy of plant-microbe interactions. *Ann. Microbiol.* **2019**, *69*, 307–320. [[CrossRef](#)]
126. Virk, A.L.; Lin, B.-J.; Kan, Z.-R.; Qi, J.-Y.; Dang, Y.P.; Lal, R.; Zhao, X.; Zhang, H.-L. Simultaneous effects of legume cultivation on carbon and nitrogen accumulation in soil. In *Advances in Agronomy*; Elsevier: Amsterdam, The Netherlands, 2022; Volume 171, pp. 75–110.
127. Stajković, O.; Delić, D.; Jošić, D.; Kuzmanović, D.; Rasulić, N.; Knežević-Vukčević, J. Improvement of common bean growth by co-inoculation with *Rhizobium* and plant growth-promoting bacteria. *Rom. Biotechnol. Lett.* **2011**, *16*, 5919–5926.
128. Rana, A.; Kabi, S.R.; Verma, S.; Adak, A.; Pal, M.; Shivay, Y.S.; Prasanna, R.; Nain, L. Prospecting plant growth promoting bacteria and cyanobacteria as options for enrichment of macro- and micronutrients in grains in rice-wheat cropping sequence. *Cogent Food. Agric.* **2015**, *1*, 1037379. [[CrossRef](#)]
129. Morales, A.; Alvear, M.; Valenzuela, E.; Rubio, R.; Borie, F. Effect of inoculation with *Penicillium albidum*, a phosphate-solubilizing fungus, on the growth of *Trifolium pratense* cropped in a volcanic soil. *J. Basic Microbiol.* **2007**, *47*, 275–280. [[CrossRef](#)] [[PubMed](#)]
130. Hungria, M.; Nogueira, M.A.; Araujo, R.S.; Hungria, M.; Nogueira, M.A.; Araujo, R.S. Soybean seed co-inoculation with *Bradyrhizobium* spp. and *Azospirillum brasilense*: A new biotechnological tool to improve yield and sustainability. *Am. J. Plant Sci.* **2015**, *6*, 811–817. [[CrossRef](#)]
131. Alkooranee, J.T.; Aledan, T.R.; Ali, A.K.; Lu, G.; Zhang, X.; Wu, J.; Fu, C.; Li, M. Detecting the hormonal pathways in oilseed rape behind induced systemic resistance by *Trichoderma harzianum* TH12 to *Sclerotinia sclerotiorum*. *PLoS ONE* **2017**, *12*, e0168850. [[CrossRef](#)]
132. Leonetti, P.; Zonno, M.C.; Molinari, S.; Altomare, C. Induction of SA-signaling pathway and ethylene biosynthesis in *Trichoderma harzianum*-treated tomato plants after infection of the root-knot nematode *Meloidogyne incognita*. *Plant Cell Rep.* **2017**, *36*, 621–631. [[CrossRef](#)]
133. Qin, S.; Zhang, Y.-J.; Yuan, B.; Xu, P.-Y.; Xing, K.; Wang, J.; Jiang, J.-H. Isolation of ACC deaminase-producing habitat-adapted symbiotic bacteria associated with halophyte *Limonium sinense* (Girard) Kuntze and evaluating their plant growth-promoting activity under salt stress. *Plant Soil* **2014**, *374*, 753–766. [[CrossRef](#)]
134. Rafique, H.M.; Khan, M.Y.; Asghar, H.N.; Ahmad Zahir, Z.; Nadeem, S.M.; Sohaib, M.; Alotaibi, F.; Al-Barakah, F.N.I. Converging alfalfa (*Medicago sativa* L.) and petroleum hydrocarbon acclimated ACC-deaminase containing bacteria for phytoremediation of petroleum hydrocarbon contaminated soil. *Int. J. Phytoremediation* **2022**. [[CrossRef](#)]
135. Vurukonda, S.S.K.P.; Vardharajula, S.; Shrivastava, M.; SkZ, A. Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. *Microbiol. Res.* **2016**, *184*, 13–24. [[CrossRef](#)]
136. Glick, B.R.; Gamalero, E. Recent developments in the study of plant microbiomes. *Microorganisms* **2021**, *9*, 1533. [[CrossRef](#)] [[PubMed](#)]
137. Gobbato, E.; Wang, E.; Higgins, G.; Bano, S.A.; Henry, C.; Schultze, M.; Oldroyd, G.E.D. *RAM1* and *RAM2* function and expression during arbuscular mycorrhizal symbiosis and *Aphanomyces euteiches* colonization. *Plant Signal. Behav.* **2013**, *8*, e26049. [[CrossRef](#)] [[PubMed](#)]
138. Keshavan, N.D.; Chowdhary, P.K.; Haines, D.C.; González, J.E. L-canavanine made by *Medicago sativa* interferes with quorum sensing in *Sinorhizobium meliloti*. *J. Bacteriol.* **2005**, *187*, 8427–8436. [[CrossRef](#)] [[PubMed](#)]
139. Kravchenko, L.V.; Azarova, T.S.; Leonova-Erko, E.I.; Shaposhnikov, A.I.; Makarova, N.M.; Tikhonovich, I.A. Root exudates of tomato plants and their effect on the growth and antifungal activity of *Pseudomonas* strains. *Microbiology* **2003**, *72*, 37–41. [[CrossRef](#)]
140. Rasmann, S.; Köllner, T.G.; Degenhardt, J.; Hiltbold, I.; Toepfer, S.; Kuhlmann, U.; Gershenzon, J.; Turlings, T.C.J. Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature* **2005**, *434*, 732–737. [[CrossRef](#)] [[PubMed](#)]
141. Zhang, N.; Wang, D.; Liu, Y.; Li, S.; Shen, Q.; Zhang, R. Effects of different plant root exudates and their organic acid components on chemotaxis, biofilm formation and colonization by beneficial rhizosphere-associated bacterial strains. *Plant Soil* **2014**, *374*, 689–700. [[CrossRef](#)]
142. Danhorn, T.; Fuqua, C. Biofilm formation by plant-associated bacteria. *Annu. Rev. Microbiol.* **2007**, *61*, 401–422. [[CrossRef](#)]
143. Jiménez Bremont, J.; Marina, M.; de la Luz Guerrero-González, M.; Rossi, F.; Sánchez-Rangel, D.; Rodríguez-Kessler, M.; Ruiz, O.; Gárriz, A. Physiological and molecular implications of plant polyamine metabolism during biotic interactions. *Front. Plant Sci.* **2014**, *5*, 95. [[CrossRef](#)]
144. Liu, Z.; Beskrovnaya, P.; Melnyk, R.A.; Hossain, S.S.; Khorasani, S.; O’Sullivan, L.R.; Wiesmann, C.L.; Bush, J.; Richard, J.D.; Haney, C.H. A genome-wide screen identifies genes in rhizosphere-associated *Pseudomonas* required to evade plant defenses. *mBio* **2018**, *9*, e00433-18. [[CrossRef](#)]
145. Nelson, M.S.; Sadowsky, M.J. Secretion systems and signal exchange between nitrogen-fixing rhizobia and legumes. *Front. Plant Sci.* **2015**, *6*, 491. [[CrossRef](#)]
146. Wang, Q.; Liu, J.; Zhu, H. Genetic and molecular mechanisms underlying symbiotic specificity in legume-rhizobium interactions. *Front. Plant Sci.* **2018**, *9*, 313. [[CrossRef](#)] [[PubMed](#)]
147. Hugoni, M.; Luis, P.; Guyonnet, J.; el Zahar Haichar, F. Plant host habitat and root exudates shape fungal diversity. *Mycorrhiza* **2018**, *28*, 451–463. [[CrossRef](#)] [[PubMed](#)]

148. Hu, L.; Robert, C.A.M.; Cadot, S.; Zhang, X.; Ye, M.; Li, B.; Manzo, D.; Chervet, N.; Steinger, T.; van der Heijden, M.G.A.; et al. Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. *Nat. Commun.* **2018**, *9*, 2738. [[CrossRef](#)] [[PubMed](#)]
149. Kawasaki, A.; Dennis, P.G.; Forstner, C.; Raghavendra, A.K.H.; Mathesius, U.; Richardson, A.E.; Delhaize, E.; Gilliam, M.; Watt, M.; Ryan, P.R. Manipulating exudate composition from root apices shapes the microbiome throughout the root system. *Plant Physiol.* **2021**, *187*, 2279–2295. [[CrossRef](#)]
150. Kudjordjie, E.N.; Sapkota, R.; Nicolaisen, M. *Arabidopsis* assemble distinct root-associated microbiomes through the synthesis of an array of defense metabolites. *PLoS ONE* **2021**, *16*, e0259171. [[CrossRef](#)]
151. Qu, Q.; Li, Y.; Zhang, Z.; Cui, H.; Zhao, Q.; Liu, W.; Lu, T.; Qian, H. Effects of S-metolachlor on wheat (*Triticum aestivum* L.) seedling root exudates and the rhizosphere microbiome. *J. Hazard. Mater.* **2021**, *411*, 125137. [[CrossRef](#)]
152. Weisskopf, L.; Abou-Mansour, E.; Fromin, N.; Tomasi, N.; Santelia, D.; Edelkott, I.; Neumann, G.; Aragno, M.; Tabacchi, R.; Martinoia, E. White lupin has developed a complex strategy to limit microbial degradation of secreted citrate required for phosphate acquisition. *Plant Cell Environ.* **2006**, *29*, 919–927. [[CrossRef](#)]
153. EL Zahar Haichar, F.; Marol, C.; Berge, O.; Rangel-Castro, J.I.; Prosser, J.I.; Balesdent, J.; Heulin, T.; Achouak, W. Plant host habitat and root exudates shape soil bacterial community structure. *ISME J.* **2008**, *2*, 1221–1230. [[CrossRef](#)]
154. Sasse, J.; Martinoia, E.; Northen, T. Feed your friends: Do plant exudates shape the root microbiome? *Trends Plant Sci.* **2018**, *23*, 25–41. [[CrossRef](#)]
155. Cai, T.; Cai, W.; Zhang, J.; Zheng, H.; Tsou, A.M.; Xiao, L.; Zhong, Z.; Zhu, J. Host legume-exuded antimetabolites optimize the symbiotic rhizosphere. *Mol. Microbiol.* **2009**, *73*, 507–517. [[CrossRef](#)]
156. Mardani-Korran, H.; Nakayasu, M.; Yamazaki, S.; Aoki, Y.; Kaida, R.; Motobayashi, T.; Kobayashi, M.; Ohkama-Ohtsu, N.; Oikawa, Y.; Sugiyama, A.; et al. L-canavanine, a root exudate from hairy vetch (*Vicia villosa*) drastically affecting the soil microbial community and metabolite pathways. *Front. Microbiol.* **2021**, *12*, 701796. [[CrossRef](#)] [[PubMed](#)]
157. Stringlis, I.A.; Yu, K.; Feussner, K.; de Jonge, R.; van Bentum, S.; van Verk, M.C.; Berendsen, R.L.; Bakker, P.A.H.M.; Feussner, I.; Pieterse, C.M.J. MYB72-dependent coumarin exudation shapes root microbiome assembly to promote plant health. *PNAS* **2018**, *115*, E5213–E5222. [[CrossRef](#)] [[PubMed](#)]
158. Baune, M.; Kang, K.; Schenkeveld, W.D.C.; Kraemer, S.M.; Hayen, H.; Weber, G. Importance of oxidation products in coumarin-mediated Fe(hydr)oxide mineral dissolution. *BioMetals* **2020**, *33*, 305–321. [[CrossRef](#)] [[PubMed](#)]
159. Toljander, J.F.; Lindahl, B.D.; Paul, L.R.; Elfstrand, M.; Finlay, R.D. Influence of arbuscular mycorrhizal mycelial exudates on soil bacterial growth and community structure. *FEMS Microbiol. Ecol.* **2007**, *61*, 295–304. [[CrossRef](#)] [[PubMed](#)]
160. Badri, D.V.; Quintana, N.; el Kassis, E.G.; Kim, H.K.; Choi, Y.H.; Sugiyama, A.; Verpoorte, R.; Martinoia, E.; Manter, D.K.; Vivanco, J.M. An ABC transporter mutation alters root exudation of phytochemicals that provoke an overhaul of natural soil microbiota. *Plant Physiol.* **2009**, *151*, 2006–2017. [[CrossRef](#)] [[PubMed](#)]
161. Vives-Peris, V.; de Ollas, C.; Gómez-Cadenas, A.; Pérez-Clemente, R.M. Root exudates: From plant to rhizosphere and beyond. *Plant Cell Rep.* **2020**, *39*, 3–17. [[CrossRef](#)]
162. Volkov, V.; Schwenke, H. A quest for mechanisms of plant root exudation brings new results and models, 300 years after Hales. *Plants* **2020**, *10*, 38. [[CrossRef](#)]
163. Kapilan, R.; Vaziri, M.; Zwiasek, J.J. Regulation of aquaporins in plants under stress. *Biol. Res.* **2018**, *51*, 4. [[CrossRef](#)]
164. Dietz, S.; von Bülow, J.; Beitz, E.; Nehls, U. The aquaporin gene family of the ectomycorrhizal fungus *Laccaria bicolor*: Lessons for symbiotic functions. *N. Phytol.* **2011**, *190*, 927–940. [[CrossRef](#)]
165. Hwang, J.H.; Ellingson, S.R.; Roberts, D.M. Ammonia permeability of the soybean nodulin 26 channel. *FEBS Lett.* **2010**, *584*, 4339–4343. [[CrossRef](#)]
166. Masalkar, P.; Wallace, I.S.; Hwang, J.H.; Roberts, D.M. Interaction of cytosolic glutamine synthetase of soybean root nodules with the C-terminal domain of the symbiosome membrane nodulin 26 aquaglyceroporin. *J. Biol. Chem.* **2010**, *285*, 23880–23888. [[CrossRef](#)] [[PubMed](#)]
167. Janczak, K.; Dąbrowska, G.; Znajewska, Z.; Hryniewicz, K. Effect of bacterial inoculation on the growth of miscanthus and bacterial and fungal density in the polymer-containing soil. Part 2. Non-biodegradable polymers. *Chem. Ind.* **2014**, *93*, 2222–2225.
168. Janczak, K.; Dąbrowska, G.; Znajewska, Z.; Hryniewicz, K. Effect of bacterial inoculation on the growth of miscanthus and bacterial and fungal density in the polymer-containing soil. Part 1. Biodegradable polymers. *Chem. Ind.* **2014**, *93*, 2218–2221.
169. Janczak, K.; Dąbrowska, G.B.; Raszewska-Kaczor, A.; Kaczor, D.; Hryniewicz, K.; Richert, A. Biodegradation of the plastics PLA and PET in cultivated soil with the participation of microorganisms and plants. *Int. Biodeterior. Biodegrad.* **2020**, *155*, 105087. [[CrossRef](#)]
170. Afzal, M.; Yousaf, S.; Reichenauer, T.G.; Sessitsch, A. The inoculation method affects colonization and performance of bacterial inoculant strains in the phytoremediation of soil contaminated with diesel oil. *Int. J. Phytoremediation* **2012**, *14*, 35–47. [[CrossRef](#)] [[PubMed](#)]
171. Yousaf, S.; Afzal, M.; Reichenauer, T.G.; Brady, C.L.; Sessitsch, A. Hydrocarbon degradation, plant colonization and gene expression of alkane degradation genes by endophytic *Enterobacter ludwigii* strains. *Environ. Pollut.* **2011**, *159*, 2675–2683. [[CrossRef](#)] [[PubMed](#)]
172. Louvel, B.; Cébron, A.; Leyval, C. Root exudates affect phenanthrene biodegradation, bacterial community and functional gene expression in sand microcosms. *Int. Biodeterior. Biodegrad.* **2011**, *65*, 947–953. [[CrossRef](#)]

173. Chen, L.; Yang, X.; Raza, W.; Li, J.; Liu, Y.; Qiu, M.; Zhang, F.; Shen, Q. *Trichoderma harzianum* SQR-T037 rapidly degrades allelochemicals in rhizospheres of continuously cropped cucumbers. *Appl. Microbiol. Biotechnol.* **2011**, *89*, 1653–1663. [[CrossRef](#)]
174. Wang, Y.; Li, H.; Feng, G.; Du, L.; Zeng, D. Biodegradation of diuron by an endophytic fungus *Neurospora intermedia* DP8-1 isolated from sugarcane and its potential for remediating diuron-contaminated soils. *PLoS ONE* **2017**, *12*, e0182556. [[CrossRef](#)]
175. Abdelghany, T.M.; El-Ghany Tm, A.; Masmali, I.A. Fungal biodegradation of organophosphorus insecticides and their impact on soil microbial population. *J. Plant Pathol. Microbiol.* **2016**, *7*, 1000349.
176. Guerrero, R.; Margulis, L.; Berlanga, M. Symbiogenesis: The holobiont as a unit of evolution. *Int. Microbiol.* **2013**, *16*, 133–143. [[PubMed](#)]
177. Trivedi, P.; Leach, J.E.; Tringe, S.G.; Sa, T.; Singh, B.K. Plant–microbiome interactions: From community assembly to plant health. *Nat. Rev. Microbiol.* **2020**, *18*, 607–621. [[CrossRef](#)] [[PubMed](#)]
178. Santhanam, R.; Luu, V.T.; Weinhold, A.; Goldberg, J.; Oh, Y.; Baldwin, I.T. Native root-associated bacteria rescue a plant from a sudden-wilt disease that emerged during continuous cropping. *Proc. Natl. Acad. Sci. USA* **2015**, *112*, E5013–E5120. [[CrossRef](#)]
179. Garbeva, P.; Silby, M.W.; Raaijmakers, J.M.; Levy, S.B.; de Boer, W. Transcriptional and antagonistic responses of *Pseudomonas fluorescens* Pf0-1 to phylogenetically different bacterial competitors. *ISME J.* **2011**, *5*, 973–985. [[CrossRef](#)] [[PubMed](#)]
180. Arendt, K.R.; Hockett, K.L.; Araldi-Brondolo, S.J.; Baltrus, D.A.; Arnold, A.E. Isolation of endohyphal bacteria from foliar Ascomycota and in vitro establishment of their symbiotic associations. *Appl. Environ. Microbiol.* **2016**, *82*, 2943–2949. [[CrossRef](#)]
181. Hoffman, M.T.; Gunatilaka, M.K.; Wijeratne, K.; Gunatilaka, L.; Arnold, A.E. Endohyphal bacterium enhances production of indole-3-acetic acid by a foliar fungal endophyte. *PLoS ONE* **2013**, *8*, e73132. [[CrossRef](#)]
182. Márquez, L.M.; Redman, R.S.; Rodriguez, R.J.; Roossinck, M.J. A virus in a fungus in a plant: Three-way symbiosis required for thermal tolerance. *Science* **2007**, *315*, 513–515. [[CrossRef](#)]
183. Rodriguez, R.J.; Henson, J.; van Volkenburgh, E.; Hoy, M.; Wright, L.; Beckwith, F.; Kim, Y.-O.; Redman, R.S. Stress tolerance in plants via habitat-adapted symbiosis. *ISME J.* **2008**, *2*, 404–416. [[CrossRef](#)]
184. Chen, H.; Wu, H.; Yan, B.; Zhao, H.; Liu, F.; Zhang, H.; Sheng, Q.; Miao, F.; Liang, Z. Core microbiome of medicinal plant *Salvia miltiorrhiza* seed: A rich reservoir of beneficial microbes for secondary metabolism? *Int. J. Mol. Sci.* **2018**, *19*, 672. [[CrossRef](#)]
185. Redford, A.J.; Bowers, R.M.; Knight, R.; Linhart, Y.; Fierer, N. The ecology of the phyllosphere: Geographic and phylogenetic variability in the distribution of bacteria on tree leaves: Biogeography of phyllosphere bacterial communities. *Environ. Microbiol.* **2010**, *12*, 2885–2893. [[CrossRef](#)]
186. Germida, J.; Siciliano, S. Taxonomic diversity of bacteria associated with the roots of modern, recent and ancient wheat cultivars. *Biol. Fertil. Soils* **2001**, *33*, 410–415.
187. Churchland, C.; Grayston, S.J. Specificity of plant-microbe interactions in the tree mycorrhizosphere biome and consequences for soil C cycling. *Front. Microbiol.* **2014**, *5*, 261. [[CrossRef](#)] [[PubMed](#)]
188. Grubisha, L.C.; Trappe, J.M.; Molina, R.; Spatafora, J.W. Biology of the ectomycorrhizal genus *Rhizopogon*. VI. Re-examination of infrageneric relationships inferred from phylogenetic analyses of ITS sequences. *Mycologia* **2002**, *94*, 607–619. [[CrossRef](#)]
189. Young, J.P.W.; Johnston, A.W.B. The evolution of specificity in the legume-rhizobium symbiosis. *Trends Ecol. Evol.* **1989**, *4*, 341–349. [[CrossRef](#)]
190. Wicaksono, W.A.; Cernava, T.; Berg, C.; Berg, G. Bog ecosystems as a playground for plant–microbe coevolution: Bryophytes and vascular plants harbour functionally adapted bacteria. *Microbiome* **2021**, *9*, 170. [[CrossRef](#)] [[PubMed](#)]
191. Cobian, G.M.; Egan, C.P.; Amend, A.S. Plant–microbe specificity varies as a function of elevation. *ISME J.* **2019**, *13*, 2778–2788. [[CrossRef](#)]
192. Salas-González, I.; Reyt, G.; Flis, P.; Custódio, V.; Gopaulchan, D.; Bakhoun, N.; Dew, T.P.; Suresh, K.; Franke, R.B.; Dangel, J.L.; et al. Coordination between microbiota and root endodermis supports plant mineral nutrient homeostasis. *Science* **2021**, *371*, eabd0695. [[CrossRef](#)]
193. Compant, S.; Samad, A.; Faist, H.; Sessitsch, A. A review on the plant microbiome: Ecology, functions, and emerging trends in microbial application. *J. Adv. Res.* **2019**, *19*, 29–37. [[CrossRef](#)]
194. Mitter, B.; Pfaffenbichler, N.; Sessitsch, A. Plant–microbe partnerships in 2020. *Microb. Biotechnol.* **2016**, *9*, 635–640. [[CrossRef](#)]
195. Abdelfattah, A.; Wisniewski, M.; Schena, L.; Tack, A.J.M. Experimental evidence of microbial inheritance in plants and transmission routes from seed to phyllosphere and root. *Environ. Microbiol.* **2021**, *23*, 2199–2214. [[CrossRef](#)]
196. Sánchez-López, A.S.; Pintelon, I.; Stevens, V.; Imperato, V.; Timmermans, J.P.; González-Chávez, C.; Carrillo-González, R.; van hamme, J.; Vangronsveld, J.; Thijs, S. Seed endophyte microbiome of *Crotalaria pumila* unpeeled: Identification of plant-beneficial methylobacteria. *Int. J. Mol. Sci.* **2018**, *19*, 291. [[CrossRef](#)]
197. Coleman-Derr, D.; Desgarnes, D.; Fonseca-Garcia, C.; Gross, S.; Clingenpeel, S.; Woyke, T.; North, G.; Visel, A.; Partida-Martinez, L.P.; Tringe, S.G. Plant compartment and biogeography affect microbiome composition in cultivated and native *Agave* species. *N. Phytol.* **2016**, *209*, 798–811. [[CrossRef](#)] [[PubMed](#)]
198. Zarraindia, I.; Owens, S.M.; Weisenhorn, P.; West, K.; Hampton-Marcell, J.; Lax, S.; Bokulich, N.A.; Mills, D.A.; Martin, G.; Taghavi, S.; et al. The soil microbiome influences grapevine-associated microbiota. *mBio* **2015**, *6*, e02527-14. [[CrossRef](#)] [[PubMed](#)]
199. De Souza, R.S.C.; Okura, V.K.; Armanhi, J.S.L.; Jorrín, B.; Lozano, N.; da Silva, M.J.; González-Guerrero, M.; de Araújo, L.M.; Verza, N.C.; Bagheri, H.C.; et al. Unlocking the bacterial and fungal communities assemblages of sugarcane microbiome. *Sci. Rep.* **2016**, *6*, 28774. [[CrossRef](#)] [[PubMed](#)]

200. Shade, A.; McManus, P.S.; Handelsman, J. Unexpected diversity during community succession in the apple flower microbiome. *mBio* **2013**, *4*, e00602-12. [[CrossRef](#)] [[PubMed](#)]
201. Wipf, H.M.L.; Bui, T.N.; Coleman-Derr, D. Distinguishing between the impacts of heat and drought stress on the root microbiome of *Sorghum bicolor*. *Phytobiomes J.* **2021**, *5*, 166–176. [[CrossRef](#)]
202. Nuccio, E.E.; Anderson-Furgeson, J.; Estera, K.Y.; Pett-Ridge, J.; de Valpine, P.; Brodie, E.L.; Firestone, M.K. Climate and edaphic controllers influence rhizosphere community assembly for a wild annual grass. *Ecology* **2016**, *97*, 1307–1318. [[CrossRef](#)]
203. Gargouri, M.; Karray, F.; Chebaane, A.; Mhiri, N.; Partida-Martínez, L.P.; Sayadi, S.; Mliki, A. Increasing aridity shapes beta diversity and the network dynamics of the belowground fungal microbiome associated with *Opuntia ficus-indica*. *Sci. Total Environ.* **2021**, *773*, 145008. [[CrossRef](#)]
204. Lau, J.A.; Lennon, J.T. Rapid responses of soil microorganisms improve plant fitness in novel environments. *Proc. Natl. Acad. Sci. USA* **2012**, *109*, 14058–14062. [[CrossRef](#)]
205. Zhang, Y.; Jiang, W.; Li, Q.; Xu, W.; Wang, J.; Hu, J.; Zhang, Z. Soil nutrient levels determine the variation of bacterial communities in the rhizosphere of rice under different conditions of climate and genotype. *Appl. Soil Ecol.* **2021**, *167*, 104025. [[CrossRef](#)]
206. Pii, Y.; Borruso, L.; Brusetti, L.; Crechchio, C.; Cesco, S.; Mimmo, T. The interaction between iron nutrition, plant species and soil type shapes the rhizosphere microbiome. *Plant Physiol. Biochem.* **2016**, *99*, 39–48. [[CrossRef](#)] [[PubMed](#)]
207. Rastogi, G.; Sbodio, A.; Tech, J.J.; Suslow, T.V.; Coaker, G.L.; Leveau, J.H.J. Leaf microbiota in an agroecosystem: Spatiotemporal variation in bacterial community composition on field-grown lettuce. *ISME J.* **2012**, *6*, 1812–1822. [[CrossRef](#)] [[PubMed](#)]
208. Gontia-Mishra, I.; Sapre, S.; Deshmukh, R.; Sikdar, S.; Tiwari, S. Microbe-mediated drought tolerance in plants: Current developments and future challenges. In *Plant Microbiomes for Sustainable Agriculture*; Yadav, A.N., Singh, J., Rastegari, A.A., Yadav, N., Eds.; Springer: Berlin/Heidelberg, Germany, 2020; pp. 351–379.
209. Naylor, D.; DeGraaf, S.; Purdom, E.; Coleman-Derr, D. Drought and host selection influence bacterial community dynamics in the grass root microbiome. *ISME J.* **2017**, *11*, 2691–2704. [[CrossRef](#)] [[PubMed](#)]
210. Santos-Medellín, C.; Edwards, J.; Liechty, Z.; Nguyen, B.; Sundaresan, V. Drought stress results in a compartment-specific restructuring of the rice root-associated microbiomes. *mBio* **2017**, *8*, e00764-17. [[CrossRef](#)] [[PubMed](#)]
211. Nelson, A.R.; Narrowe, A.B.; Rhoades, C.C.; Fegel, T.S.; Daly, R.A.; Roth, H.K.; Chu, R.K.; Amundson, K.K.; Young, R.B.; Steindorff, A.S.; et al. Wildfire-dependent changes in soil microbiome diversity and function. *Nat. Microbiol.* **2022**, *7*, 1419–1430. [[CrossRef](#)]
212. Wei, F.; Feng, H.; Zhang, D.; Feng, Z.; Zhao, L.; Zhang, Y.; Deakin, G.; Peng, J.; Zhu, H.; Xu, X. Composition of rhizosphere microbial communities associated with healthy and *Verticillium* wilt diseased cotton plants. *Front. Microbiol.* **2021**, *12*, 618169. [[CrossRef](#)]
213. Lazcano, C.; Boyd, E.; Holmes, G.; Hewavitharana, S.; Pasulka, A.; Ivors, K. The rhizosphere microbiome plays a role in the resistance to soil-borne pathogens and nutrient uptake of strawberry cultivars under field conditions. *Sci. Rep.* **2021**, *11*, 3188. [[CrossRef](#)]
214. Kong, H.G.; Kim, B.K.; Song, G.C.; Lee, S.; Ryu, C.-M. Aboveground whitefly infestation-mediated reshaping of the root microbiota. *Front. Microbiol.* **2016**, *7*, 1314. [[CrossRef](#)]
215. Turnbaugh, P.J.; Ley, R.E.; Hamady, M.; Fraser-Liggett, C.M.; Knight, R.; Gordon, J.I. The human microbiome project. *Nature* **2007**, *449*, 804–810. [[CrossRef](#)]
216. Neu, A.T.; Allen, E.E.; Roy, K. Defining and quantifying the core microbiome: Challenges and prospects. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, e2104429118. [[CrossRef](#)]
217. Lay, C.-Y.; Bell, T.H.; Hamel, C.; Harker, K.N.; Mohr, R.; Greer, C.W.; Yergeau, É.; St-Arnaud, M. Canola root-associated microbiomes in the canadian prairies. *Front. Microbiol.* **2018**, *9*, 1188. [[CrossRef](#)] [[PubMed](#)]
218. Hassani, M.A.; Durán, P.; Hacquard, S. Microbial interactions within the plant holobiont. *Microbiome* **2018**, *6*, 58. [[CrossRef](#)]
219. Agler, M.T.; Ruhe, J.; Kroll, S.; Morhenn, C.; Kim, S.T.; Weigel, D.; Kemen, E.M. Microbial hub taxa link host and abiotic factors to plant microbiome variation. *PLoS Biol.* **2016**, *14*, e1002352. [[CrossRef](#)] [[PubMed](#)]
220. Niu, B.; Paulson, J.N.; Zheng, X.; Kolter, R. Simplified and representative bacterial community of maize roots. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, E2450–E2459. [[CrossRef](#)] [[PubMed](#)]
221. Margulis, L.; Fester, R. Symbiosis as a source of evolutionary innovation: Speciation and morphogenesis. In *Cambridge Mass; MIT Press: Cambridge, MA, USA*, 1991; pp. 1–14.
222. Teixeira, P.J.P.; Colaianni, N.R.; Fitzpatrick, C.R.; Dangel, J.L. Beyond pathogens: Microbiota interactions with the plant immune system. *Curr. Opin. Microbiol.* **2019**, *49*, 7–17. [[CrossRef](#)] [[PubMed](#)]
223. Harman, G.E.; Uphoff, N. Symbiotic root-endophytic soil microbes improve crop productivity and provide environmental benefits. *Scientifica* **2019**, *2019*, 9106395. [[CrossRef](#)] [[PubMed](#)]
224. Zilber-Rosenberg, I.; Rosenberg, E. Role of microorganisms in the evolution of animals and plants: The hologenome theory of evolution. *FEMS Microbiol. Rev.* **2008**, *32*, 723–735. [[CrossRef](#)]
225. Rosenberg, E.; Koren, O.; Reshef, L.; Efrony, R.; Zilber-Rosenberg, I. The role of microorganisms in coral health, disease and evolution. *Nat. Rev. Microbiol.* **2007**, *5*, 355–362. [[CrossRef](#)]
226. Rosenberg, E.; Zilber-Rosenberg, I. The hologenome concept of evolution after 10 years. *Microbiome* **2018**, *6*, 78. [[CrossRef](#)]

227. Romero, F.M.; Marina, M.; Pieckenstein, F.L.; Rossi, F.R.; Gonzalez, M.E.; Vignatti, P.; Gárriz, A. Gaining insight into plant responses to beneficial and pathogenic microorganisms using metabolomic and transcriptomic approaches. In *Metabolic Engineering for Bioactive Compounds: Strategies and Processes*; Springer: Berlin/Heidelberg, Germany, 2017; pp. 113–140.
228. Dangl, J.L.; Horvath, D.M.; Staskawicz, B.J. Pivoting the plant immune system from dissection to deployment. *Science* **2013**, *341*, 746–751. [[CrossRef](#)]
229. Jubic, L.M.; Saile, S.; Furzer, O.J.; el Kasmi, F.; Dangl, J.L. Help wanted: Helper NLRs and plant immune responses. *Curr. Opin. Plant Biol.* **2019**, *50*, 82–94. [[CrossRef](#)] [[PubMed](#)]
230. Block, A.; Li, G.; Fu, Z.Q.; Alfano, J.R. Phytopathogen type III effector weaponry and their plant targets. *Curr. Opin. Plant Biol.* **2008**, *11*, 396–403. [[CrossRef](#)] [[PubMed](#)]
231. Thomma, B.P.H.J.; Nürnberger, T.; Joosten, M.H.A.J. Of PAMPs and effectors: The blurred PTI-ETI dichotomy. *Plant Cell* **2011**, *23*, 4–15. [[CrossRef](#)]
232. Yuan, M.; Jiang, Z.; Bi, G.; Nomura, K.; Liu, M.; Wang, Y.; Cai, B.; Zhou, J.M.; He, S.Y.; Xin, X.F. Pattern-recognition receptors are required for NLR-mediated plant immunity. *Nature* **2021**, *592*, 105–109. [[CrossRef](#)]
233. Teixeira, P.J.P.L.; Colaianni, N.R.; Law, T.F.; Conway, J.M.; Gilbert, S.; Li, H.; Salas-González, I.; Panda, D.; del Risco, N.M.; Finkel, O.M.; et al. Specific modulation of the root immune system by a community of commensal bacteria. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, e2100678118. [[CrossRef](#)]
234. Bai, B.; Liu, W.; Qiu, X.; Zhang, J.; Zhang, J.; Bai, Y. The root microbiome: Community assembly and its contributions to plant fitness. *J. Integr. Plant Biol.* **2022**, *64*, 230–243. [[CrossRef](#)]
235. Zhou, F.; Emonet, A.; Dénervaud Tendon, V.; Marhavy, P.; Wu, D.; Lahaye, T.; Geldner, N. Co-occurrence of damage and microbial patterns controls localized immune responses in roots. *Cell* **2020**, *180*, 440–453.e18. [[CrossRef](#)]
236. Saravanakumar, K.; Fan, L.; Fu, K.; Yu, C.; Wang, M.; Xia, H.; Sun, J.; Li, Y.; Chen, J. Cellulase from *Trichoderma harzianum* interacts with roots and triggers induced systemic resistance to foliar disease in maize. *Sci. Rep.* **2016**, *6*, 35543. [[CrossRef](#)] [[PubMed](#)]
237. Zahir, Z.A.; Ghani, U.; Naveed, M.; Nadeem, S.M.; Asghar, H.N. Comparative effectiveness of *Pseudomonas* and *Serratia* sp. containing ACC-deaminase for improving growth and yield of wheat (*Triticum aestivum* L.) under salt-stressed conditions. *Arch. Microbiol.* **2009**, *191*, 415–424. [[CrossRef](#)]
238. Adhikari, P.; Pandey, A. Phosphate solubilization potential of endophytic fungi isolated from *Taxus wallichiana* Zucc. roots. *Rhizosphere* **2019**, *9*, 2–9. [[CrossRef](#)]
239. Zhao, L.; Zhang, Y.Q. Effects of phosphate solubilization and phytohormone production of *Trichoderma asperellum* Q1 on promoting cucumber growth under salt stress. *J. Integr. Agric.* **2015**, *14*, 1588–1597. [[CrossRef](#)]
240. Fochi, V.; Chitarra, W.; Kohler, A.; Voyron, S.; Singan, V.R.; Lindquist, E.A.; Barry, K.W.; Girlanda, M.; Grigoriev, I.V.; Martin, F.; et al. Fungal and plant gene expression in the *Tulasnella calospora*–*Serapias vomeracea* symbiosis provides clues about nitrogen pathways in orchid mycorrhizas. *N. Phytol.* **2017**, *213*, 365–379. [[CrossRef](#)] [[PubMed](#)]
241. Li, T.; Hu, Y.J.; Hao, Z.P.; Li, H.; Wang, Y.S.; Chen, B.D. First cloning and characterization of two functional aquaporin genes from an arbuscular mycorrhizal fungus *Glomus intraradices*. *N. Phytol.* **2013**, *197*, 617–630. [[CrossRef](#)] [[PubMed](#)]
242. Gujar, P.D.; Bhavsar, K.P.; Khire, J.M. Effect of phytase from *Aspergillus niger* on plant growth and mineral assimilation in wheat (*Triticum aestivum* Linn.) and its potential for use as a soil amendment. *J. Sci. Food Agric.* **2013**, *93*, 2242–2247. [[CrossRef](#)] [[PubMed](#)]
243. Viterbo, A.; Landau, U.; Kim, S.; Chernin, L.; Chet, I. Characterization of ACC deaminase from the biocontrol and plant growth-promoting agent *Trichoderma asperellum* T203. *FEMS Microbiol. Lett.* **2010**, *305*, 42–48. [[CrossRef](#)]
244. Viterbo, A.; Chet, I. *TasHyd1*, a new hydrophobin gene from the biocontrol agent *Trichoderma asperellum*, is involved in plant root colonization. *Mol. Plant Pathol.* **2006**, *7*, 249–258. [[CrossRef](#)]
245. Samolski, I.; Rincón, A.M.; Pinzón, L.M.; Viterbo, A.; Monte, E. The *qid74* gene from *Trichoderma harzianum* has a role in root architecture and plant biofertilization. *Microbiology* **2012**, *158*, 129–138. [[CrossRef](#)]
246. Helber, N.; Wippel, K.; Sauer, N.; Schaarschmidt, S.; Hause, B.; Requena, N. A versatile monosaccharide transporter that operates in the arbuscular mycorrhizal fungus *Glomus* sp is crucial for the symbiotic relationship with plants. *Plant Cell* **2011**, *23*, 3812–3823. [[CrossRef](#)]
247. Viterbo, A.; Wiest, A.; Brotman, Y.; Chet, I.; Kenerley, C. The 18mer peptaibols from *Trichoderma virens* elicit plant defence responses. *Mol. Plant Pathol.* **2007**, *8*, 737–746. [[CrossRef](#)]
248. Rubio, M.B.; Hermosa, R.; Reino, J.L.; Collado, I.G.; Monte, E. Thctf1 transcription factor of *Trichoderma harzianum* is involved in 6-pentyl-2H-pyran-2-one production and antifungal activity. *Fungal Genet. Biol.* **2009**, *46*, 17–27. [[CrossRef](#)]
249. Kubicek, C.P.; Herrera-Estrella, A.; Seidl-Seiboth, V.; Martinez, D.A.; Druzhinina, I.S.; Thon, M.; Zeilinger, S.; Casas-Flores, S.; Horwitz, B.A.; Mukherjee, P.K.; et al. Comparative genome sequence analysis underscores mycoparasitism as the ancestral life style of *Trichoderma*. *Genome Biol.* **2011**, *12*, R40. [[CrossRef](#)] [[PubMed](#)]
250. Brotman, Y.; Briff, E.; Viterbo, A.; Chet, I. Role of swollenin, an expansin-like protein from *Trichoderma*, in plant root colonization. *Plant Physiol.* **2008**, *147*, 779–789. [[CrossRef](#)] [[PubMed](#)]
251. Vargas, W.A.; Djonović, S.; Sukno, S.A.; Kenerley, C.M. Dimerization controls the activity of fungal elicitors that trigger systemic resistance in plants. *JBC* **2008**, *283*, 19804–19815. [[CrossRef](#)] [[PubMed](#)]
252. Djonović, S.; Vargas, W.A.; Kolomiets, M.V.; Horndeski, M.; Wiest, A.; Kenerley, C.M. A proteinaceous elicitor Sm1 from the beneficial fungus *Trichoderma virens* is required for induced systemic resistance in maize. *Plant Physiol.* **2007**, *145*, 875–889. [[CrossRef](#)]

253. Nelkner, J.; Tejerizo, G.T.; Hassa, J.; Lin, T.W.; Witte, J.; Verwaaijen, B.; Winkler, A.; Bunk, B.; Spröer, C.; Overmann, J.; et al. Genetic potential of the biocontrol agent *Pseudomonas brassicacearum* (Formerly *P. trivialis*) 3Re2-7 unraveled by genome sequencing and mining, comparative genomics and transcriptomics. *Genes* **2019**, *10*, 601. [\[CrossRef\]](#)
254. Glick, B.R.; Jacobson, C.B.; Schwarze, M.K.; Pasternak, J.J. 1-Aminocyclopropane-1-carboxylic acid deaminase mutants of the plant growth promoting rhizobacterium *Pseudomonas putida* GR12-2 do not stimulate canola root elongation. *Can. J. Microbiol.* **2011**, *40*, 911–915. [\[CrossRef\]](#)
255. Blaha, D.; Prigent-Combaret, C.; Mirza, M.S.; Moëgne-Loccoz, Y. Phylogeny of the 1-aminocyclopropane-1-carboxylic acid deaminase-encoding gene *acdS* in phytobeneficial and pathogenic *Proteobacteria* and relation with strain biogeography. *FEMS Microbiol. Ecol.* **2006**, *56*, 455–470. [\[CrossRef\]](#)
256. Taghavi, S.; van der Lelie, D.; Hoffman, A.; Zhang, Y.B.; Walla, M.D.; Vangronsveld, J.; Newman, L.; Monchy, S. Genome sequence of the plant growth promoting endophytic bacterium *Enterobacter* sp. 638. *PLoS Genet.* **2010**, *6*, e1000943. [\[CrossRef\]](#)
257. Suryadi, Y.; Susilowati, D.N.; Lestari, P.; Priyatno, T.P.; Samudra, I.M.; Hikmawati, N.; Mubarik, D.N.R.; Mubarik, N.R. Characterization of bacterial isolates producing chitinase and glucanase for biocontrol of plant fungal pathogens. *J. Agric. Technol.* **2014**, *10*, 983–999.
258. Gupta, C.P.; Kumar, B.; Dubey, R.C.; Maheshwari, D.K. Chitinase-mediated destructive antagonistic potential of *Pseudomonas aeruginosa* GRC1 against *Sclerotinia sclerotiorum* causing stem rot of peanut. *BioControl* **2006**, *51*, 821–835. [\[CrossRef\]](#)
259. Ramette, A.; Frapoli, M.; Defago, G.; Moëgne-Loccoz, Y. Phylogeny of HCN synthase-encoding *hcnBC* genes in biocontrol fluorescent pseudomonads and its relationship with host plant species and HCN synthesis ability. *Mol. Plant Microbe Interact.* **2003**, *16*, 525–535. [\[CrossRef\]](#) [\[PubMed\]](#)
260. Zimmer, W.; Hundeshagen, B.; Niederau, E. Demonstration of the indolepyruvate decarboxylase gene homologue in different auxin-producing species of the Enterobacteriaceae. *Can. J. Microbiol.* **1994**, *40*, 1072–1076. [\[CrossRef\]](#) [\[PubMed\]](#)
261. Ryu, R.J.; Patten, C.L. Aromatic amino acid-dependent expression of indole-3-pyruvate decarboxylase is regulated by TyrR in *Enterobacter cloacae* UW5. *J. Bacteriol.* **2008**, *190*, 7200–7208. [\[CrossRef\]](#)
262. Spaepen, S.; Versées, W.; Gocke, D.; Pohl, M.; Steyaert, J.; Vanderleyden, J. Characterization of phenylpyruvate decarboxylase, involved in auxin production of *Azospirillum brasilense*. *J. Bacteriol.* **2007**, *189*, 7626. [\[CrossRef\]](#)
263. Poza-Carrión, C.; Jiménez-Vicente, E.; Navarro-Rodríguez, M.; Echavarrri-Erasun, C.; Rubio, L.M. Kinetics of *nif* gene expression in a nitrogen-fixing bacterium. *J. Bacteriol.* **2014**, *196*, 595–603. [\[CrossRef\]](#) [\[PubMed\]](#)
264. Steenhoudt, O.; Vanderleyden, J. *Azospirillum*, a free-living nitrogen-fixing bacterium closely associated with grasses: Genetic, biochemical and ecological aspects. *FEMS Microbiol. Rev.* **2000**, *24*, 487–506. [\[CrossRef\]](#)
265. Satyanarayana, S.D.V.; Krishna, M.S.R.; Pavan Kumar, P.; Jeerreddy, S. In silico structural homology modeling of *nif* A protein of rhizobial strains in selective legume plants. *J. Genet. Eng. Biotechnol.* **2018**, *16*, 731–737. [\[CrossRef\]](#)
266. Woźniak, M.; Gałazka, A.; Tyśkiewicz, R.; Jaroszuk-ściseł, J. Endophytic bacteria potentially promote plant growth by synthesizing different metabolites and their phenotypic/physiological profiles in the Biolog GEN III MicroPlate™ Test. *Int. J. Mol. Sci.* **2019**, *20*, 5283. [\[CrossRef\]](#)
267. Sherathia, D.; Dey, R.; Thomas, M.; Dalsania, T.; Savsani, K.; Pal, K.K. Biochemical and molecular characterization of DAPG-producing plant growthpromoting rhizobacteria (PGPR) of groundnut (*Arachis hypogaea* L.). *Legum. Res. Int. J.* **2016**, *39*, 614–622.
268. Lynch, D.; O'Brien, J.; Welch, T.; Clarke, P.; Cuív, P.O.; Crosa, J.H.; O'Connell, M. Genetic organization of the region encoding regulation, biosynthesis, and transport of rhizobactin 1021, a siderophore produced by *Sinorhizobium meliloti*. *J. Bacteriol.* **2001**, *183*, 2576–2585. [\[CrossRef\]](#)
269. Dong, H.; Beer, S.V. Riboflavin induces disease resistance in plants by activating a novel signal transduction pathway. *Phytopathology* **2000**, *90*, 801–811. [\[CrossRef\]](#) [\[PubMed\]](#)
270. Xie, S.S.; Wu, H.J.; Zang, H.Y.; Wu, L.M.; Zhu, Q.Q.; Gao, X.W. Plant growth promotion by spermidine-producing *Bacillus subtilis* OKB105. *Mol. Plant Microbe Interact.* **2014**, *27*, 655–663. [\[CrossRef\]](#) [\[PubMed\]](#)
271. Aasfar, A.; Bargaz, A.; Yaakoubi, K.; Hilali, A.; Bennis, I.; Zeroual, Y.; Meftah Kadmiri, I. Nitrogen fixing *Azotobacter* species as potential soil biological enhancers for crop nutrition and yield stability. *Front. Microbiol.* **2021**, *12*, 354. [\[CrossRef\]](#)
272. Soumare, A.; Diedhiou, A.G.; Thuita, M.; Hafidi, M.; Ouhdouch, Y.; Gopalakrishnan, S.; Kouisni, L. Exploiting biological nitrogen fixation: A route towards a sustainable agriculture. *Plants* **2020**, *9*, 1011. [\[CrossRef\]](#)
273. Ji, J.; Yuan, D.; Jin, C.; Wang, G.; Li, X.; Guan, C. Enhancement of growth and salt tolerance of rice seedlings (*Oryza sativa* L.) by regulating ethylene production with a novel halotolerant PGPR strain *Glutamicibacter* sp. YD01 containing ACC deaminase activity. *Acta Physiol. Plant.* **2020**, *42*, 42. [\[CrossRef\]](#)
274. Kumar, S.; Chandra, R.; Keswani, C.; Minkina, T.; Mandzhieva, S.; Voloshina, M.; Meena, M. *Trichoderma viride*—Mediated modulation of oxidative stress network in potato challenged with *Alternaria solani*. *J. Plant Growth Regul.* **2022**, 1–18. [\[CrossRef\]](#)
275. Kumar, A.; Singh, S.; Mukherjee, A.; Rastogi, R.P.; Verma, J.P. Salt-tolerant plant growth-promoting *Bacillus pumilus* strain JPVS11 to enhance plant growth attributes of rice and improve soil health under salinity stress. *Microbiol. Res.* **2021**, *242*, 126616. [\[CrossRef\]](#)
276. Jain, A.; Singh, A.; Singh, S.; Singh, H.B. Microbial consortium-induced changes in oxidative stress markers in pea plants challenged with *Sclerotinia sclerotiorum*. *J. Plant Growth Regul.* **2013**, *32*, 388–398. [\[CrossRef\]](#)

277. Singh, S.P.; Gupta, R.; Gaur, R.; Srivastava, A.K. *Streptomyces* spp. alleviate *Rhizoctonia solani*-mediated oxidative stress in *Solanum lycopersicon*. *Ann. Appl. Biol.* **2016**, *168*, 232–242. [[CrossRef](#)]
278. Islam, F.; Yasmeen, T.; Arif, M.S.; Ali, S.; Ali, B.; Hameed, S.; Zhou, W. Plant growth promoting bacteria confer salt tolerance in *Vigna radiata* by up-regulating antioxidant defense and biological soil fertility. *Plant Growth Regul.* **2016**, *80*, 23–36. [[CrossRef](#)]
279. Hashem, A.; Alqarawi, A.A.; Radhakrishnan, R.; Al-Arjani, A.-B.F.; Aldehaish, H.A.; Egamberdieva, D.; Abd Allah, E.F. Arbuscular mycorrhizal fungi regulate the oxidative system, hormones and ionic equilibrium to trigger salt stress tolerance in *Cucumis sativus* L. *Saudi J. Biol. Sci.* **2018**, *25*, 1102–1114. [[CrossRef](#)] [[PubMed](#)]
280. Mierek-Adamska, A.; Kotowicz, K.; Goc, A.; Boniecka, J.; Berdychowska, J.; Dąbrowska, G.B. Potential involvement of rapeseed (*Brassica napus* L.) metallothioneins in the hydrogen peroxide-induced regulation of seed vigour. *J. Agron. Crop Sci.* **2019**, *205*, 598–607. [[CrossRef](#)]
281. Hassinen, V.H.; Tervahauta, A.I.; Schat, H.; Kärenlampi, S.O. Plant metallothioneins-metal chelators with ROS scavenging activity? *Plant Biol.* **2011**, *13*, 225–232. [[CrossRef](#)] [[PubMed](#)]
282. Gutiérrez-Mañero, F.J.; Ramos-Solano, B.; Probanza, A.; Mehouchi, J.; Tadeo, F.R.; Talon, M. The plant-growth-promoting rhizobacteria *Bacillus pumilus* and *Bacillus licheniformis* produce high amounts of physiologically active gibberellins. *Physiol. Plant* **2001**, *111*, 206–211. [[CrossRef](#)]
283. Cassán, F.; Perrig, D.; Sgroy, V.; Masciarelli, O.; Penna, C.; Luna, V. *Azospirillum brasilense* Az39 and *Bradyrhizobium japonicum* E109, inoculated singly or in combination, promote seed germination and early seedling growth in corn (*Zea mays* L.) and soybean (*Glycine max* L.). *Eur. J. Soil Biol.* **2009**, *45*, 28–35. [[CrossRef](#)]
284. Perrig, D.; Boiero, M.L.; Masciarelli, O.A.; Penna, C.; Ruiz, O.A.; Cassán, F.D.; Luna, M.V. Plant-growth-promoting compounds produced by two agronomically important strains of *Azospirillum brasilense*, and implications for inoculant formulation. *Appl. Microbiol. Biotechnol.* **2007**, *75*, 1143–1150. [[CrossRef](#)]
285. Timmusk, S.; Nicander, B.; Granhall, U.; Tillberg, E. Cytokinin production by *Paenibacillus polymyxa*. *Soil Biol. Biochem.* **1999**, *31*, 1847–1852. [[CrossRef](#)]
286. García de Salamone, I.E.; Hynes, R.K.; Nelson, L.M. Cytokinin production by plant growth promoting rhizobacteria and selected mutants. *Can. J. Microbiol.* **2011**, *47*, 404–411. [[CrossRef](#)]
287. Sorokan, A.; Veselova, S.; Benkovskaya, G.; Maksimov, I. Endophytic strain *Bacillus subtilis* 26D increases levels of phytohormones and repairs growth of potato plants after Colorado potato beetle damage. *Plants* **2021**, *10*, 923. [[CrossRef](#)]
288. Park, Y.-G.; Mun, B.-G.; Kang, S.-M.; Hussain, A.; Shahzad, R.; Seo, C.-W.; Kim, A.-Y.; Lee, S.-U.; Oh, K.Y.; Lee, D.Y.; et al. *Bacillus aryabhatai* SRB02 tolerates oxidative and nitrosative stress and promotes the growth of soybean by modulating the production of phytohormones. *PLoS ONE* **2017**, *12*, e0173203. [[CrossRef](#)]
289. Dixit, R.; Agrawal, L.; Gupta, S.; Kumar, M.; Yadav, S.; Chauhan, P.S.; Nautiyal, C.S. Southern blight disease of tomato control by 1-aminocyclopropane-1-carboxylate (ACC) deaminase producing *Paenibacillus lentimorbus* B-30488. *Plant Signal. Behav.* **2016**, *11*, e1113363. [[CrossRef](#)] [[PubMed](#)]
290. Nascimento, F.X.; Vicente, C.S.L.; Barbosa, P.; Espada, M.; Glick, B.R.; Mota, M.; Oliveira, S. Evidence for the involvement of ACC deaminase from *Pseudomonas putida* UW4 in the biocontrol of pine wilt disease caused by *Bursaphelenchus xylophilus*. *BioControl* **2013**, *58*, 427–433. [[CrossRef](#)]
291. Ravanbakhsh, M.; Sasidharan, R.; Voesenek, L.A.C.J.; Kowalchuk, G.A.; Jousset, A. ACC deaminase-producing rhizosphere bacteria modulate plant responses to flooding. *J. Ecol.* **2017**, *105*, 979–986. [[CrossRef](#)]
292. Carlos, M.-H.J.; Stefani, P.-V.Y.; Janette, A.-M.; Melani, M.-S.S.; Gabriela, P.-O. Assessing the effects of heavy metals in ACC deaminase and IAA production on plant growth-promoting bacteria. *Microbiol. Res.* **2016**, *188–189*, 53–61. [[CrossRef](#)] [[PubMed](#)]
293. Lindström, K.; Mousavi, S.A. Effectiveness of nitrogen fixation in rhizobia. *Microb. Biotechnol.* **2020**, *13*, 1314–1335. [[CrossRef](#)]
294. Yang, J.; Kloepper, J.W.; Ryu, C.-M. Rhizosphere bacteria help plants tolerate abiotic stress. *Trends Plant. Sci.* **2009**, *14*, 1–4. [[CrossRef](#)]
295. Figueiredo, M.V.B.; Burity, H.A.; Martínez, C.R.; Chanway, C.P. Alleviation of drought stress in the common bean (*Phaseolus vulgaris* L.) by co-inoculation with *Paenibacillus polymyxa* and *Rhizobium tropici*. *Appl. Soil Ecol.* **2008**, *40*, 182–188. [[CrossRef](#)]
296. Philippot, L.; Raaijmakers, J.M.; Lemanceau, P.; van der Putten, W.H. Going back to the roots: The microbial ecology of the rhizosphere. *Nat. Rev. Microbiol.* **2013**, *11*, 789–799. [[CrossRef](#)]
297. Kafle, A.; Cope, K.; Rath, R.; Krishna Yakha, J.; Subramanian, S.; Bücking, H.; Garcia, K. Harnessing soil microbes to improve plant phosphate efficiency in cropping systems. *Agronomy* **2019**, *9*, 127. [[CrossRef](#)]
298. Linu, M.S.; Stephen, J.; Jisha, M.S. Phosphate solubilizing *Gluconacetobacter* sp., *Burkholderia* sp. and their potential interaction with cowpea (*Vigna unguiculata* (L.) Walp.). *Int. J. Agric. Res.* **2009**, *4*, 79–87. [[CrossRef](#)]
299. Selvakumar, G.; Mohan, M.; Kundu, S.; Gupta, A.D.; Joshi, P.; Nazim, S.; Gupta, H.S. Cold tolerance and plant growth promotion potential of *Serratia marcescens* strain SRM (MTCC 8708) isolated from flowers of summer squash (*Cucurbita pepo*). *Let. Appl. Microbiol.* **2008**, *46*, 171–175. [[CrossRef](#)] [[PubMed](#)]
300. Parmar, P.; Sindhu, S.S. Potassium solubilization by rhizosphere bacteria: Influence of nutritional and environmental conditions. *J. Microbiol. Res.* **2013**, *3*, 25–31.
301. Gouda, S.; Kerry, R.G.; Das, G.; Paramithiotis, S.; Shin, H.S.; Patra, J.K. Revitalization of plant growth promoting rhizobacteria for sustainable development in agriculture. *Microbiol. Res.* **2018**, *206*, 131–140. [[CrossRef](#)] [[PubMed](#)]

302. Ali, A.; Javaid, A.; Shoaib, A.; Khan, I.H. Effect of soil amendment with *Chenopodium album* dry biomass and two *Trichoderma* species on growth of chickpea var. Noor 2009 in *Sclerotium rolfsii* contaminated soil. *Egypt. J. Biol. Pest Control* **2020**, *30*, 102. [CrossRef]
303. Xiao, Y.; Wang, X.; Chen, W.; Huang, Q. Isolation and identification of three potassium-solubilizing bacteria from rape rhizospheric soil and their effects on ryegrass. *Geomicrobiol. J.* **2017**, *34*, 873–880. [CrossRef]
304. Basak, B.B.; Biswas, D.R. Influence of potassium solubilizing microorganism (*Bacillus mucilaginosus*) and waste mica on potassium uptake dynamics by sudan grass (*Sorghum vulgare* Pers.) grown under two Alfisols. *Plant Soil* **2009**, *317*, 235–255. [CrossRef]
305. Raji, M.; Thangavelu, M. Isolation and screening of potassium solubilizing bacteria from saxicolous habitat and their impact on tomato growth in different soil types. *Arch. Microbiol.* **2021**, *203*, 3147–3161. [CrossRef]
306. Bityutskii, N.; Yakkonen, K.; Petrova, A.; Nadporozhskaya, M. Xylem sap mineral analyses as a rapid method for estimation plant-availability of Fe, Zn and Mn in carbonate soils: A case study in cucumber. *J. Soil Sci. Plant Nutr.* **2017**, *17*, 279–290. [CrossRef]
307. Colombo, C.; Palumbo, G.; He, J.Z.; Pinton, R.; Cesco, S. Review on iron availability in soil: Interaction of Fe minerals, plants, and microbes. *J. Soils Sediments* **2014**, *14*, 538–548. [CrossRef]
308. Rani, N.; Kaur, S.; Nitu, R.; Rajinder, K.; Sukhminderjit, K. Zinc solubilizing bacteria to augment soil fertility—A comprehensive review. *Int. Microbiol.* **2020**, *8*, 38–44.
309. Li, R.-X.; Cai, F.; Pang, G.; Shen, Q.-R.; Li, R.; Chen, W. Solubilisation of phosphate and micronutrients by *Trichoderma harzianum* and its relationship with the promotion of tomato plant growth. *PLoS ONE* **2015**, *10*, e0130081. [CrossRef] [PubMed]
310. Singh, D.; Geat, N.; Rajawat, M.V.S.; Prasanna, R.; Kar, A.; Singh, A.M.; Saxena, A.K. Prospecting endophytes from different Fe or Zn accumulating wheat genotypes for their influence as inoculants on plant growth, yield, and micronutrient content. *Ann. Microbiol.* **2018**, *68*, 815–833. [CrossRef]
311. Ögüt, M.; Er, F. Micronutrient composition of field-grown dry bean and wheat inoculated with *Azospirillum* and *Trichoderma*. *J. Plant Nutr. Soil Sci.* **2006**, *169*, 699–703. [CrossRef]
312. Durán, P.; Acuña, J.J.; Armada, E.; López-Castillo, O.M.; Cornejo, P.; Mora, M.L.; Azcón, R. Inoculation with selenobacteria and arbuscular mycorrhizal fungi to enhance selenium content in lettuce plants and improve tolerance against drought stress. *J. Soil Sci. Plant Nutr.* **2016**, *16*, 211–225. [CrossRef]
313. De Valença, A.W.; Bake, A.; Brouwer, I.D.; Giller, K.E. Agronomic biofortification of crops to fight hidden hunger in sub-Saharan Africa. *Glob. Food Sec.* **2017**, *12*, 8–14. [CrossRef]
314. Díaz-Gómez, J.; Twyman, R.M.; Zhu, C.; Farré, G.; Serrano, J.C.; Portero-Otin, M.; Muñoz, P.; Sandmann, G.; Capell, T.; Christou, P. Biofortification of crops with nutrients: Factors affecting utilization and storage. *Curr. Opin. Biotechnol.* **2017**, *44*, 115–123. [CrossRef]
315. Khush, G.S.; Lee, S.; Cho, J.I.; Jeon, J.S. Biofortification of crops for reducing malnutrition. *Plant Biotechnol. Rep.* **2012**, *6*, 195–202. [CrossRef]
316. Cabrefiga, J.; Bonaterra, A.; Montesinos, E. Mechanisms of antagonism of *Pseudomonas fluorescens* EPS62e against *Erwinia amylovora*, the casual agent of fire blight. *Int. Microbiol.* **2007**, *10*, 123132.
317. Kinsella, K.; Schulthess, C.P.; Morris, T.F.; Stuart, J.D. Rapid quantification of *Bacillus subtilis* antibiotics in the rhizosphere. *Soil Biol. Biochem.* **2009**, *41*, 374–379. [CrossRef]
318. Bais, H.P.; Fall, R.; Vivanco, J.M. Biocontrol of *Bacillus subtilis* against infection of *Arabidopsis* roots by *Pseudomonas syringae* is facilitated by biofilm formation and surfactin production. *Plant Physiol.* **2004**, *134*, 307–319. [CrossRef]
319. Liu, X.; Bimerew, M.; Ma, Y.; Müller, H.; Ovadis, M.; Eberl, L.; Berg, G.; Chernin, L. Quorum-sensing signaling is required for production of the antibiotic pyrrolnitrin in a rhizospheric biocontrol strain of *Serratia plymuthica*. *FEMS Microbiol. Lett.* **2007**, *270*, 299–305. [CrossRef] [PubMed]
320. Kurze, S.; Bahl, H.; Dahl, R.; Berg, G. Biological control of fungal strawberry diseases by *Serratia plymuthica* HRO-C48. *Plant Dis.* **2001**, *85*, 529–534. [CrossRef] [PubMed]
321. Chen, Y.; Wang, J.; Yang, N.; Wen, Z.; Sun, X.; Chai, Y.; Ma, Z. Wheat microbiome bacteria can reduce virulence of a plant pathogenic fungus by altering histone acetylation. *Nat. Commun.* **2018**, *9*, 3429. [CrossRef] [PubMed]
322. Du Jardin, P. Plant biostimulants: Definition, concept, main categories and regulation. *Sci. Hortic.* **2015**, *196*, 3–14. [CrossRef]
323. Mandal, S.; Mitra, A. Reinforcement of cell wall in roots of *Lycopersicon esculentum* through induction of phenolic compounds and lignin by elicitors. *Physiol. Mol. Plant Pathol.* **2007**, *71*, 201–209. [CrossRef]
324. Egusa, M.; Matsui, H.; Urakami, T.; Okuda, S.; Ifuku, S.; Nakagami, H.; Kaminaka, H. Chitin nanofiber elucidates the elicitor activity of polymeric chitin in plants. *Front. Plant Sci.* **2015**, *6*, 1098. [CrossRef] [PubMed]
325. Proietti, S.; Giangrande, C.; Amoresano, A.; Pucci, P.; Molinaro, A.; Bertini, L.; Caporale, C.; Caruso, C. *Xanthomonas campestris* lipooligosaccharides trigger innate immunity and oxidative burst in *Arabidopsis*. *Plant Physiol. Biochem.* **2014**, *85*, 51–62. [CrossRef]
326. Nowak, A.; Tyśkiewicz, R.; Wiater, A.; Jaroszuk-ściseł, J. (1→3)- α -D-glucooligosaccharides as elicitors influencing the activity of plant resistance pathways in wheat tissues. *Agronomy* **2022**, *12*, 1170. [CrossRef]
327. Ramkissoon, A.; Francis, J.; Bowrin, V.; Ramjegathesh, R.; Ramsubhag, A.; Jayaraman, J. Bio-efficacy of a chitosan based elicitor on *Alternaria solani* and *Xanthomonas vesicatoria* infections in tomato under tropical conditions. *Ann. Appl. Biol.* **2016**, *169*, 274–283. [CrossRef]

328. Qiu, H.; Su, L.; Wang, H.; Zhang, Z. Chitosan elicitation of saponin accumulation in *Psammosilene tunicoides* hairy roots by modulating antioxidant activity, nitric oxide production and differential gene expression. *Plant Physiol. Biochem.* **2021**, *166*, 115–127. [[CrossRef](#)]
329. Aziz, A.; Poinssot, B.; Daire, X.; Adrian, M.; Bézier, A.; Lambert, B.; Joubert, J.M.; Pugin, A. Laminarin elicits defense responses in grapevine and induces protection against *Botrytis cinerea* and *Plasmopara viticola*. *Mol. Plant Microbe Interact.* **2003**, *16*, 1118–1128. [[CrossRef](#)] [[PubMed](#)]
330. Cashel, M.; Gallant, J. Two compounds implicated in the function of the RC gene of *Escherichia coli*. *Nature* **1969**, *221*, 838–841. [[CrossRef](#)] [[PubMed](#)]
331. Boniecka, J.; Prusińska, J.; Dąbrowska, G.B.; Goc, A. Within and beyond the stringent response-RSH and (p)ppGpp in plants. *Planta* **2017**, *246*, 817–842. [[CrossRef](#)] [[PubMed](#)]
332. Dąbrowska, G.; Prusińska, J.; Goc, A. The stringent response—Bacterial mechanism of an adaptive stress response. *Adv. Biochem.* **2006**, *52*, 87–93.
333. Berdychowska, J.; Boniecka, J.; Dąbrowska, G.B. The stringent response and its involvement in the reactions of bacterial cells to stress. *Adv. Microbiol.* **2019**, *58*, 127–142. [[CrossRef](#)]
334. Irving, S.E.; Corrigan, R.M.Y.R. Triggering the stringent response: Signals responsible for activating (p)ppGpp synthesis in bacteria. *Microbiology* **2018**, *164*, 268–276. [[CrossRef](#)]
335. Irving, S.E.; Choudhury, N.R.; Corrigan, R.M. The stringent response and physiological roles of (pp)pGpp in bacteria. *Nat. Rev. Microbiol.* **2021**, *19*, 256–271. [[CrossRef](#)]
336. Sun, D.; Lee, G.; Lee, J.H.; Kim, H.Y.; Rhee, H.W.; Park, S.Y.; Kim, K.J.; Kim, Y.; Kim, B.Y.; Hong, J.I.; et al. A metazoan ortholog of SpoT hydrolyzes ppGpp and functions in starvation responses. *Nat. Struct. Mol. Biol.* **2010**, *17*, 1188–1194. [[CrossRef](#)]
337. Sanchez-Vazquez, P.; Dewey, C.N.; Kitten, N.; Ross, W.; Gourse, R.L. Genome-wide effects on *Escherichia coli* transcription from ppGpp binding to its two sites on RNA polymerase. *Proc. Natl. Acad. Sci. USA* **2019**, *116*, 8310–8319. [[CrossRef](#)]
338. Seyfzadeh, M.; Keener, J.; Nomura, M. spoT-dependent accumulation of guanosine tetraphosphate in response to fatty acid starvation in *Escherichia coli*. *Proc. Natl. Acad. Sci. USA* **1993**, *90*, 11004–11008. [[CrossRef](#)]
339. Battesti, A.; Bouveret, E. Acyl carrier protein/SpoT interaction, the switch linking SpoT-dependent stress response to fatty acid metabolism. *Mol. Microbiol.* **2006**, *62*, 1048–1063. [[CrossRef](#)] [[PubMed](#)]
340. Vinella, D.; Albrecht, C.; Cashel, M.; D’Ari, R. Iron limitation induces SpoT-dependent accumulation of ppGpp in *Escherichia coli*. *Mol. Microbiol.* **2005**, *56*, 958–970. [[CrossRef](#)] [[PubMed](#)]
341. Flardh, K.; Axberg, T.; Albertson, N.H.; Kjelleberg, S. Stringent control during carbon starvation of marine *Vibrio* sp. strain S14: Molecular cloning, nucleotide sequence, and deletion of the *relA* gene. *J. Bacteriol.* **1994**, *176*, 5949–5957. [[CrossRef](#)] [[PubMed](#)]
342. Brown, D.R.; Barton, G.; Pan, Z.; Buck, M.; Wigneshweraraj, S. Nitrogen stress response and stringent response are coupled in *Escherichia coli*. *Nat. Commun.* **2014**, *5*, 4115. [[CrossRef](#)] [[PubMed](#)]
343. Sivapragasam, S.; Deochand, D.K.; Meariman, J.K.; Grove, A. The stringent response induced by phosphate limitation promotes purine salvage in *Agrobacterium fabrum*. *Biochemistry* **2017**, *56*, 5831–5843. [[CrossRef](#)] [[PubMed](#)]
344. English, B.P.; Haurlyliuk, V.; Sanamrad, A.; Tankov, S.; Dekker, N.H.; Elf, J. Single-molecule investigations of the stringent response machinery in living bacterial cells. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, E365–E373. [[CrossRef](#)]
345. Gallant, J.; Palmer, L.; Pao, C.C. Anomalous synthesis of ppGpp in growing cells. *Cell* **1977**, *11*, 181–185. [[CrossRef](#)]
346. Thackray, P.D.; Moir, A. SigM, an extracytoplasmic function sigma factor of *Bacillus subtilis*, is activated in response to cell wall antibiotics, ethanol, heat, acid, and superoxide stress. *J. Bacteriol.* **2003**, *185*, 3491–3498. [[CrossRef](#)]
347. Anderson, K.L.; Roux, C.M.; Olson, M.W.; Luong, T.T.; Lee, C.Y.; Olson, R.; Dunman, P.M. Characterizing the effects of inorganic acid and alkaline shock on the *Staphylococcus aureus* transcriptome and messenger RNA turnover. *FEMS Immunol. Med. Microbiol.* **2010**, *60*, 208–250. [[CrossRef](#)]
348. Heizmann, P.; Howell, S.H. Synthesis of ppGpp and chloroplast ribosomal RNA in *Chlamydomonas reinhardtii*. *Biochim. Biophys. Acta* **1978**, *517*, 115–124. [[CrossRef](#)]
349. Van der Biezen, E.A. *Arabidopsis RelA/SpoT* homologs implicate (p)ppGpp in plant signaling. *Proc. Natl. Acad. Sci. USA* **2000**, *97*, 3747–3752. [[CrossRef](#)] [[PubMed](#)]
350. Givens, R.M.; Lin, M.-H.; Taylor, D.J.; Mechold, U.; Berry, J.O.; Hernandez, V.J. Inducible expression, enzymatic activity, and origin of higher plant homologues of bacterial RelA/SpoT stress proteins in *Nicotiana tabacum*. *J. Biol. Chem.* **2004**, *279*, 7495–7504. [[CrossRef](#)] [[PubMed](#)]
351. Xiong, L.; Lee, M.W.; Qi, M.; Yang, Y. Identification of defense-related rice genes by suppression subtractive hybridization and differential screening. *Mol. Plant Microbe Interact.* **2001**, *14*, 685–692. [[CrossRef](#)] [[PubMed](#)]
352. Dąbrowska, G.B.; Prusińska, J.; Goc, A. Identification of the RSH gene cDNA (*RelA-SpoT* homolog) involved in *Pharbitis nil* response to stress conditions. *Zesz. Probl. Postępów Nauk. Rol.* **2006**, *509*, 343–351.
353. Yamada, A.; Tsutsumi, K.; Tanimoto, S.; Ozeki, Y. Plant *RelA/SpoT* homolog confers salt tolerance in *Escherichia coli* and *Saccharomyces cerevisiae*. *Plant Cell Physiol.* **2003**, *44*, 3–9. [[CrossRef](#)]
354. Kim, T.-H.; Ok, S.H.; Kim, D.; Suh, S.-C.; Byun, M.O.; Shin, J.S. Molecular characterization of a biotic and abiotic stress resistance-related gene *RelA/SpoT* homologue (*PepRSH*) from pepper. *Plant Sci.* **2009**, *176*, 635–642. [[CrossRef](#)]
355. Sato, M.; Takahashi, T.; Ochi, K.; Matsuura, H.; Nabeta, K.; Takahashi, K. Overexpression of *RelA/SpoT* homologs, *PpRSH2a* and *PpRSH2b*, induces the growth suppression of the moss *Physcomitrella patens*. *Biosci. Biotechnol. Biochem.* **2015**, *79*, 36–44. [[CrossRef](#)]

356. Mizusawa, K.; Masuda, S.; Ohta, H. Expression profiling of four RelA/SpoT-like proteins, homologues of bacterial stringent factors, in *Arabidopsis thaliana*. *Planta* **2008**, *228*, 553–562. [[CrossRef](#)]
357. Atkinson, G.C.; Tenson, T.; Haurlyliuk, V. The RelA/SpoT Homolog (RSH) superfamily: Distribution and functional evolution of ppGpp synthetases and hydrolases across the tree of life. *PLoS ONE* **2011**, *6*, e23479. [[CrossRef](#)]
358. Shin, J.; Singal, B.; Grüber, A.; Wong, D.M.K.; Ragnathan, P.; Grüber, G. Atomic structure of the regulatory TGS domain of Rel protein from *Mycobacterium tuberculosis* and its interaction with deacylated tRNA. *FEBS Lett.* **2021**, *595*, 3006–3018. [[CrossRef](#)]
359. Tozawa, Y.; Nozawa, A.; Kanno, T.; Narisawa, T.; Masuda, S.; Kasai, K.; Nanamiya, H. Calcium-activated (p)ppGpp synthetase in chloroplasts of land plants. *J. Biol. Chem.* **2007**, *282*, 35536–35545. [[CrossRef](#)] [[PubMed](#)]
360. Ito, K.; Ito, D.; Goto, M.; Suzuki, S.; Masuda, S.; Iba, K.; Kusumi, K. Regulation of ppGpp synthesis and its impact on chloroplast biogenesis during early leaf development in rice. *Plant Cell Physiol.* **2022**, *63*, 919–931. [[CrossRef](#)] [[PubMed](#)]
361. Yamburenko, M.V.; Zubo, Y.O.; Börner, T. Abscisic acid affects transcription of chloroplast genes via protein phosphatase 2C-dependent activation of nuclear genes: Repression by guanosine-3'-5'-bisdiphosphate and activation by sigma factor 5. *Plant J.* **2015**, *82*, 1030–1041. [[CrossRef](#)] [[PubMed](#)]
362. Kasai, K.; Kanno, T.; Endo, Y.; Wakasa, K.; Tozawa, Y. Guanosine tetra- and pentaphosphate synthase activity in chloroplasts of a higher plant: Association with 70S ribosomes and inhibition by tetracycline. *Nucleic Acids Res.* **2004**, *32*, 5732–5741. [[CrossRef](#)]
363. Imamura, S.; Nomura, Y.; Takemura, T.; Pancha, I.; Taki, K.; Toguchi, K.; Tozawa, Y.; Tanaka, K. The checkpoint kinase TOR (target of rapamycin) regulates expression of a nuclear-encoded chloroplast RelA-SpoT homolog (RSH) and modulates chloroplast ribosomal RNA synthesis in a unicellular red alga. *Plant J.* **2018**, *94*, 327–339. [[CrossRef](#)]
364. Sugliani, M.; Abdelkefi, H.; Ke, H.; Bouveret, E.; Robaglia, C.; Caffarri, S.; Field, B. An ancient bacterial signaling pathway regulates chloroplast function to influence growth and development in *Arabidopsis*. *Plant Cell* **2016**, *28*, 661–679. [[CrossRef](#)]
365. Abdelkefi, H.; Sugliani, M.; Ke, H.; Harchouni, S.; Soubigou-Taconnat, L.; Citerne, S.; Mouille, G.; Fakhfakh, H.; Robaglia, C.; Field, B. Guanosine tetraphosphate modulates salicylic acid signalling and the resistance of *Arabidopsis thaliana* to turnip mosaic virus. *Mol. Plant Pathol.* **2018**, *19*, 634–646. [[CrossRef](#)]
366. Kahlau, S.; Bock, R. Plastid transcriptomics and translomics of tomato fruit development and chloroplast-to-chromoplast differentiation: Chromoplast gene expression largely serves the production of a single protein. *Plant Cell* **2008**, *20*, 856–874. [[CrossRef](#)]
367. Maekawa, M.; Honoki, R.; Ihara, Y.; Sato, R.; Oikawa, A.; Kanno, Y.; Ohta, H.; Seo, M.; Saito, K.; Masuda, S. Impact of the plastidial stringent response in plant growth and stress responses. *Nat. Plants* **2015**, *1*, 15167. [[CrossRef](#)]
368. Honoki, R.; Ono, S.; Oikawa, A.; Saito, K.; Masuda, S. Significance of accumulation of the alarmone (p)ppGpp in chloroplasts for controlling photosynthesis and metabolite balance during nitrogen starvation in *Arabidopsis*. *Photosynth. Res.* **2018**, *135*, 299–308. [[CrossRef](#)]
369. Romand, S.; Abdelkefi, H.; Lecampion, C.; Belaroussi, M.; Dussenne, M.; Ksas, B.; Citerne, S.; Caius, J.; D'alessandro, S.; Fakhfakh, H.; et al. A guanosine tetraphosphate (ppGpp) mediated brake on photosynthesis is required for acclimation to nitrogen limitation in *Arabidopsis*. *eLife* **2022**, *11*, 75041. [[CrossRef](#)]
370. Li, H.; Nian, J.; Fang, S.; Guo, M.; Huang, X.; Zhang, F.; Wang, Q.; Zhang, J.; Bai, J.; Dong, G.; et al. Regulation of nitrogen starvation responses by the alarmone (p)ppGpp in rice. *J. Genet. Genom.* **2022**, *49*, 469–480. [[CrossRef](#)] [[PubMed](#)]
371. Takahashi, K.; Kasai, K.; Ochi, K. Identification of the bacterial alarmone guanosine 5'-diphosphate 3'-diphosphate (ppGpp) in plants. *Proc. Natl. Acad. Sci. USA* **2004**, *101*, 4320–4324. [[CrossRef](#)] [[PubMed](#)]
372. Masuda, S.; Mizusawa, K.; Narisawa, T.; Tozawa, Y.; Ohta, H.; Takamiya, K.I. The bacterial stringent response, conserved in chloroplasts, controls plant fertilization. *Plant Cell Physiol.* **2008**, *49*, 135–141. [[CrossRef](#)] [[PubMed](#)]
373. Ono, S.; Suzuki, S.; Ito, D.; Tagawa, S.; Shiina, T.; Masuda, S. Plastidial (p)ppGpp synthesis by the Ca²⁺-dependent RelA-SpoT homolog regulates the adaptation of chloroplast gene expression to darkness in *Arabidopsis*. *Plant Cell Physiol.* **2021**, *61*, 2077–2086. [[CrossRef](#)]
374. Nowicki, D.; Rodzik, O.; Herman-Antosiewicz, A.; Szalewska-Pałasz, A. Isothiocyanates as effective agents against enterohemorrhagic *Escherichia coli*: Insight to the mode of action. *Sci. Rep.* **2016**, *6*, 22263. [[CrossRef](#)]
375. Mi, L.; Hood, B.L.; Stewart, N.A.; Xiao, Z.; Govind, S.; Wang, X.; Conrads, T.P.; Veenstra, T.D.; Chung, F.-L. Identification of potential protein targets of isothiocyanates by proteomics. *Chem. Res. Toxicol.* **2011**, *24*, 1735–1743. [[CrossRef](#)]
376. Mwita, L.; Chan, W.Y.; Pretorius, T.; Lyantagaye, S.L.; Lapa, S.V.; Avdeeva, L.V.; Reva, O.N. Gene expression regulation in the plant growth promoting *Bacillus atrophaeus* UCMB-5137 stimulated by maize root exudates. *Gene* **2016**, *590*, 18–28. [[CrossRef](#)]
377. Dąbrowska, G.B.; Turkan, S.; Tyłman-Mojżeszczak, W.; Mierek-Adamska, A. In silico study of the RSH (RelA/spot homologs) gene family and expression analysis in response to PGPR bacteria and salinity in *Brassica napus*. *Int. J. Mol. Sci.* **2021**, *22*, 10666. [[CrossRef](#)]
378. Chapelle, E.; Mendes, R.; Bakker, P.A.H.; Raaijmakers, J.M. Fungal invasion of the rhizosphere microbiome. *ISME J.* **2016**, *10*, 265–268. [[CrossRef](#)]
379. Manuel, J.; Berry, C.; Selin, C.; Fernando, W.G.D.; de Kievit, T.R. Repression of the antifungal activity of *Pseudomonas* sp. strain DF41 by the stringent response. *Appl. Environ. Microbiol.* **2011**, *77*, 5635–5642. [[CrossRef](#)] [[PubMed](#)]
380. Manuel, J.; Selin, C.; Dilantha Fernando, W.G.; de Kievit, T. Stringent response mutants of *Pseudomonas chlororaphis* PA23 exhibit enhanced antifungal activity against *Sclerotinia sclerotiorum* in vitro. *Microbiology* **2012**, *158*, 207–216. [[CrossRef](#)] [[PubMed](#)]

381. Selin, C.; Manuel, J.; Fernando, W.G.D.; de Kievit, T. Expression of the *Pseudomonas chlororaphis* strain PA23 Rsm system is under control of *GacA*, *RpoS*, *PsrA*, quorum sensing and the stringent response. *Biol. Control* **2014**, *69*, 24–33. [[CrossRef](#)]
382. Takeuchi, K.; Yamada, K.; Haas, D. ppGpp controlled by the *Gac/Rsm* regulatory pathway sustains biocontrol activity in *Pseudomonas fluorescens* CHA0. *Mol. Plant Microbe Interact.* **2012**, *25*, 1440–1449. [[CrossRef](#)] [[PubMed](#)]
383. Ochi, K. A *rel* mutation abolishes the enzyme induction needed for actinomycin synthesis by *Streptomyces antibioticus*. *Agric. Biol. Chem.* **2014**, *51*, 829–835.
384. Ryu, Y.G.; Wook, J.; Jin, Y.K.; Jae, Y.K.; Sang, H.L.; Kye, J.L. Stringent factor regulates antibiotics production and morphological differentiation of *Streptomyces clavuligerus*. *J. Microbiol. Biotechnol.* **2004**, *14*, 1170–1175.
385. Brechenmacher, L.; Lei, Z.; Libault, M.; Findley, S.; Sugawara, M.; Sadowsky, M.J.; Sumner, L.W.; Stacey, G. Soybean metabolites regulated in root hairs in response to the symbiotic bacterium *Bradyrhizobium japonicum*. *Plant Physiol.* **2010**, *153*, 1808–1822. [[CrossRef](#)]
386. Murray, J.D. Invasion by invitation: Rhizobial infection in legumes. *Mol. Plant Microbe Interact.* **2011**, *24*, 631–639. [[CrossRef](#)]
387. Tsyganova, A.V.; Brewin, N.J.; Tsyganov, V.E. Structure and development of the legume-rhizobial symbiotic interface in infection threads. *Cells* **2021**, *10*, 1050. [[CrossRef](#)]
388. Pérez-Giménez, J.; Iturralde, E.T.; Torres Tejerizo, G.; Quelas, J.I.; Krol, E.; Borassi, C.; Becker, A.; Estevez, J.M.; Lodeiro, A.R. A stringent-response-defective *Bradyrhizobium diazoefficiens* strain does not activate the type 3 secretion system, elicits an early plant defense response, and circumvents NH₄NO₃-induced inhibition of nodulation. *Appl. Environ. Microbiol.* **2021**, *87*, e02989–20. [[CrossRef](#)]
389. Wippel, K.; Long, S.R. Symbiotic performance of *Sinorhizobium meliloti* lacking ppGpp depends on the *Medicago* host species. *Mol. Plant Microbe Interact.* **2019**, *32*, 717–728. [[CrossRef](#)] [[PubMed](#)]
390. Wells, D.H.; Long, S.R. The *Sinorhizobium meliloti* stringent response affects multiple aspects of symbiosis. *Mol. Microbiol.* **2002**, *43*, 1115–1127. [[CrossRef](#)] [[PubMed](#)]
391. Moris, M.; Braeken, K.; Schoeters, E.; Verreth, C.; Beullens, S.; Vanderleyden, J.; Michiels, J. Effective symbiosis between *Rhizobium etli* and *Phaseolus vulgaris* requires the alarmone ppGpp. *J. Bacteriol.* **2005**, *187*, 5460–5469. [[CrossRef](#)] [[PubMed](#)]
392. Calderón-Flores, A.; du Pont, G.; Huerta-Saquero, A.; Merchant-Larios, H.; Servín-González, L.; Durán, S. The stringent response is required for amino acid and nitrate utilization, nod factor regulation, nodulation, and nitrogen fixation in *Rhizobium etli*. *J. Bacteriol.* **2005**, *187*, 5075. [[CrossRef](#)] [[PubMed](#)]
393. Qiu, X.; Gao, T.; Yang, J.; Wang, E.; Liu, L.; Yuan, H. Water-soluble humic materials modulating metabolism and triggering stress defense in *Sinorhizobium fredii*. *Microbiol. Spectr.* **2021**, *9*, e00293–21. [[CrossRef](#)] [[PubMed](#)]
394. Ancona, V.; Lee, J.H.; Chatnaparat, T.; Oh, J.; Hong, J.I.; Zhao, Y. The bacterial alarmone (p)ppGpp activates the type III secretion system in *Erwinia amylovora*. *J. Bacteriol.* **2015**, *197*, 1433–1443. [[CrossRef](#)] [[PubMed](#)]
395. Chatnaparat, T.; Li, Z.; Korban, S.S.; Zhao, Y. The bacterial alarmone (p)ppGpp is required for virulence and controls cell size and survival of *Pseudomonas syringae* on plants. *Environ. Microbiol.* **2015**, *17*, 4253–4270. [[CrossRef](#)]
396. Chatnaparat, T.; Li, Z.; Korban, S.S.; Zhao, Y. The stringent response mediated by (p)ppGpp is required for virulence of *Pseudomonas syringae* pv. tomato and its survival on tomato. *Mol. Plant Microbe Interact.* **2015**, *28*, 776–789. [[CrossRef](#)]
397. Bowden, S.D.; Hale, N.; Chung, J.C.S.; Hodgkinson, J.T.; Spring, D.R.; Welch, M. Surface swarming motility by *Pectobacterium atrosepticum* is a latent phenotype that requires O antigen and is regulated by quorum sensing. *Microbiology* **2013**, *159*, 2375–2385. [[CrossRef](#)]
398. Petrova, O.; Gorshkov, V.; Sergeeva, I.; Daminova, A.; Ageeva, M.; Gogolev, Y. Alternative scenarios of starvation-induced adaptation in *Pectobacterium atrosepticum*. *Res. Microbiol.* **2016**, *167*, 254–261. [[CrossRef](#)]
399. Zhang, Y.; Teper, D.; Xu, J.; Wang, N. Stringent response regulators (p)ppGpp and *DksA* positively regulate virulence and host adaptation of *Xanthomonas citri*. *Mol. Plant. Pathol.* **2019**, *20*, 1550–1565. [[CrossRef](#)] [[PubMed](#)]
400. Harman, G.E.; Howell, C.R.; Viterbo, A.; Chet, I.; Lorito, M. *Trichoderma* species—Opportunistic, avirulent plant symbionts. *Nat. Rev. Microbiol.* **2004**, *2*, 43–56. [[CrossRef](#)] [[PubMed](#)]
401. Wojtkowiak-Gębarowska, E. Mechanisms of biological control soil-borne plant pathogen by fungus from genus *Trichoderma*. *Adv. Microbiol.* **2006**, *45*, 261–273.
402. Bustamante, D.E.; Calderon, M.S.; Leiva, S.; Mendoza, J.E.; Arce, M.; Oliva, M. Three new species of *Trichoderma* in the Harzianum and Longibrachiatum lineages from Peruvian cacao crop soils based on an integrative approach. *Mycologia* **2021**, *113*, 1056–1072. [[CrossRef](#)]
403. Pascale, A.; Vinale, F.; Manganiello, G.; Nigro, M.; Lanzuise, S.; Ruocco, M.; Marra, R.; Lombardi, N.; Woo, S.L.; Lorito, M. *Trichoderma* and its secondary metabolites improve yield and quality of grapes. *Crop Prot.* **2017**, *92*, 176–181. [[CrossRef](#)]
404. Srivastava, S.N.; Singh, V.; Awasthi, S.K. *Trichoderma* induced improvement in growth, yield and quality of sugarcane. *Sugar Tech* **2006**, *8*, 166–169. [[CrossRef](#)]
405. Colla, G.; Roupshael, Y.; di Mattia, E.; El-Nakhel, C.; Cardarelli, M. Co-inoculation of *Glomus intraradices* and *Trichoderma atroviride* acts as a biostimulant to promote growth, yield and nutrient uptake of vegetable crops. *J. Sci. Food Agric.* **2015**, *95*, 1706–1715. [[CrossRef](#)]
406. Rudresh, D.L.; Shivaprakash, M.K.; Prasad, R.D. Effect of combined application of *Rhizobium*, phosphate solubilizing bacterium and *Trichoderma* spp. on growth, nutrient uptake and yield of chickpea (*Cicer aritenium* L.). *Appl. Soil Ecol.* **2005**, *28*, 139–146. [[CrossRef](#)]

407. Khomari, S.; Golshan-Doust, S.; Seyed-Sharifi, R.; Davari, M. Improvement of soybean seedling growth under salinity stress by biopriming of high-vigour seeds with salt-tolerant isolate of *Trichoderma harzianum*. *N. Z. J. Crop Hortic. Sci.* **2018**, *46*, 117–132. [[CrossRef](#)]
408. Asaduzzaman, M.; Alam, M.; Islam, M. Effect of *Trichoderma* on seed germination and seedling parameters of chili. *J. Sci. Found.* **2013**, *8*, 141–150. [[CrossRef](#)]
409. Vargas, W.A.; Mandawe, J.C.; Kenerley, C.M. Plant-derived sucrose is a key element in the symbiotic association between *Trichoderma virens* and maize plants. *Plant Physiol.* **2009**, *151*, 792–808. [[CrossRef](#)]
410. Brotman, Y.; Lisec, J.; Méret, M.; Chet, I.; Willmitzer, L.; Viterbo, A. Transcript and metabolite analysis of the *Trichoderma*-induced systemic resistance response to *Pseudomonas syringae* in *Arabidopsis thaliana*. *Microbiology* **2012**, *158*, 139–146. [[CrossRef](#)] [[PubMed](#)]
411. Contreras-Cornejo, H.A.; Macías-Rodríguez, L.; Vergara, A.G.; López-Bucio, J. *Trichoderma* modulates stomatal aperture and leaf transpiration through an abscisic acid-dependent mechanism in *Arabidopsis*. *J. Plant Growth Regul.* **2015**, *34*, 425–432. [[CrossRef](#)]
412. Bae, H.; Sicher, R.C.; Kim, M.S.; Kim, S.-H.; Strem, M.D.; Melnick, R.L.; Bailey, B.A. The beneficial endophyte *Trichoderma hamatum* isolate DIS 219b promotes growth and delays the onset of the drought response in *Theobroma cacao*. *J. Exp. Bot.* **2009**, *60*, 3279–3295. [[CrossRef](#)] [[PubMed](#)]
413. Shores, M.; Harman, G.E. The molecular basis of shoot responses of maize seedlings to *Trichoderma harzianum* T22 inoculation of the root: A proteomic approach. *Plant Physiol.* **2008**, *147*, 2147–2163. [[CrossRef](#)]
414. Mercl, F.; García-Sánchez, M.; Kulhánek, M.; Košnář, Z.; Száková, J.; Tlustoš, P. Improved phosphorus fertilisation efficiency of wood ash by fungal strains *Penicillium* sp. PK112 and *Trichoderma harzianum* OMG08 on acidic soil. *Appl. Soil Ecol.* **2020**, *147*, 103360. [[CrossRef](#)]
415. Fu, J.; Xiao, Y.; Wang, Y.; Liu, Z.; Yang, K. Saline-alkaline stress in growing maize seedlings is alleviated by *Trichoderma asperellum* through regulation of the soil environment. *Sci. Rep.* **2021**, *11*, 11152. [[CrossRef](#)]
416. Zhang, F.; Xu, X.; Wang, G.; Wu, B.; Xiao, Y. *Medicago sativa* and soil microbiome responses to *Trichoderma* as a biofertilizer in alkaline-saline soils. *Appl. Soil Ecol.* **2020**, *153*, 103573. [[CrossRef](#)]
417. Adams, P.; De-Leij, F.A.A.M.; Lynch, J.M. *Trichoderma harzianum* Rifai 1295-22 mediates growth promotion of crack willow (*Salix fragilis*) saplings in both clean and metal-contaminated soil. *Microb. Ecol.* **2007**, *54*, 306–313. [[CrossRef](#)]
418. López Errasquín, E.; Vázquez, C. Tolerance and uptake of heavy metals by *Trichoderma atroviride* isolated from sludge. *Chemosphere* **2003**, *50*, 137–143. [[CrossRef](#)]
419. Rajendran, L.; Raja, P.; Jegadeeswari, V.; Santhi, V.P.; Selvaraj, N. *Pseudomonas fluorescens* and *Trichoderma viride* enriched bioconsortium for the management of *Fusarium* wilt in carnation and gerbera under protected cultivation. *Indian Phytopathol.* **2014**, *67*, 77–81.
420. Ambuse, M.G.; Chatage, V.S.; Bhale, U.N. Influence of *Trichoderma* spp against *Alternaria tenuissima* inciting leaf spot of *Rumex acetosa* L. *Biosci. Discov.* **2012**, *3*, 259–262.
421. De Padua, J.C.; de la Cruz, T.E.E. Isolation and characterization of nickel-tolerant *Trichoderma* strains from marine and terrestrial environments. *J. Fungi* **2021**, *7*, 591. [[CrossRef](#)] [[PubMed](#)]
422. Sánchez-Montesinos, B.; Diánez, F.; Moreno-Gavira, A.; Gea, F.J.; Santos, M. Plant growth promotion and biocontrol of *Pythium ultimum* by saline tolerant *Trichoderma* isolates under salinity stress. *Int. J. Environ. Res. Public Health* **2019**, *16*, 2053. [[CrossRef](#)] [[PubMed](#)]
423. Shi, Z.-Z.; Miao, F.-P.; Fang, S.-T.; Yin, X.-L.; Ji, N.-Y. Sulfurated diketopiperazines from an algicolous isolate of *Trichoderma virens*. *Phytochem. Lett.* **2018**, *27*, 101–104. [[CrossRef](#)]
424. Touati, I.; Ruiz, N.; Thomas, O.; Druzhinina, I.S.; Atanasova, L.; Tabbene, O.; Elkahoui, S.; Benzekri, R.; Bouslama, L.; Pouchus, Y.F.; et al. Hyporientalin A, an anti-Candida peptaibol from a marine *Trichoderma orientale*. *World J. Microbiol. Biotechnol.* **2018**, *34*, 98. [[CrossRef](#)]
425. Zhang, C.; Wang, W.; Hu, Y.; Peng, Z.; Ren, S.; Xue, M.; Liu, Z.; Hou, J.; Xing, M.; Liu, T. A novel salt-tolerant strain *Trichoderma atroviride* HN082102.1 isolated from marine habitat alleviates salt stress and diminishes cucumber root rot caused by *Fusarium oxysporum*. *BMC Microbiol.* **2022**, *22*, 67. [[CrossRef](#)]
426. Gal-Hemed, I.; Atanasova, L.; Komon-Zelazowska, M.; Druzhinina, I.S.; Viterbo, A.; Yarden, O. Marine isolates of *Trichoderma* spp. as potential halotolerant agents of biological control for arid-zone agriculture. *Appl. Environ. Microbiol.* **2011**, *77*, 5100–5109. [[CrossRef](#)]
427. Nogueira-Lopez, G.; Greenwood, D.R.; Middleditch, M.; Winefield, C.; Eaton, C.; Steyaert, J.M.; Mendoza-Mendoza, A. The apoplasmic secretome of *Trichoderma virens* during interaction with maize roots shows an inhibition of plant defence and scavenging oxidative stress secreted proteins. *Front. Plant Sci.* **2018**, *9*, 409. [[CrossRef](#)]
428. Sofo, A.; Scopa, A.; Manfra, M.; de Nisco, M.; Tenore, G.; Troisi, J.; di Fiori, R.; Novellino, E. *Trichoderma harzianum* strain T-22 induces changes in phytohormone levels in cherry rootstocks (*Prunus cerasus* × *P. canescens*). *Plant Growth Regul.* **2011**, *65*, 421–425. [[CrossRef](#)]
429. Yedidia, I.; Shores, M.; Kerem, Z.; Benhamou, N.; Kapulnik, Y.; Chet, I. Concomitant induction of systemic resistance to *Pseudomonas syringae* pv. lachrymans in cucumber by *Trichoderma asperellum* (T-203) and accumulation of phytoalexins. *Appl. Environ. Microbiol.* **2003**, *69*, 7343–7353. [[PubMed](#)]

430. Akhter, W.; Bhuiyan, M.K.A.; Sultana, F.; Hossain, M.M. Integrated effect of microbial antagonist, organic amendment and fungicide in controlling seedling mortality (*Rhizoctonia solani*) and improving yield in pea (*Pisum sativum* L.). *Comptes Rendus. Biol.* **2015**, *338*, 21–28. [[CrossRef](#)] [[PubMed](#)]
431. Howell, C.R.; Hanson, L.E.; Stipanovic, R.D.; Puckhaber, L.S. Induction of terpenoid synthesis in cotton roots and control of *Rhizoctonia solani* by seed treatment with *Trichoderma virens*. *Phytopathology* **2000**, *90*, 248–252. [[CrossRef](#)] [[PubMed](#)]
432. Gomes, E.V.; Costa, M.D.N.; de Paula, R.G.; Ricci De Azevedo, R.; da Silva, F.L.; Noronha, E.F.; José Ulhoa, C.; Neves Monteiro, V.; Elena Cardoza, R.; Gutiérrez, S.; et al. The cerato-platanin protein Epl-1 from *Trichoderma harzianum* is involved in mycoparasitism, plant resistance induction and self cell wall protection. *Sci. Rep.* **2015**, *5*, 17998. [[CrossRef](#)] [[PubMed](#)]
433. Howell, C.R. Cotton seedling preemergence damping-off incited by *Rhizopus oryzae* and *Pythium* spp. and its biological control with *Trichoderma* spp. *Phytopathology* **2002**, *92*, 177–180. [[CrossRef](#)] [[PubMed](#)]
434. Hossain, M.M.; Hossain, N.; Sultana, F.; Mohammad, S.; Islam, N.; Khurshed, M.; Bhuiyan, A. Integrated management of Fusarium wilt of chickpea (*Cicer arietinum* L.) caused by *Fusarium oxysporum* f. sp. ciceris with microbial antagonist, botanical extract sp. ciceris with microbial antagonist, botanical extract. *Afr. J. Biotechnol.* **2016**, *12*, 4699–4706.
435. Vujanovic, V.; Goh, Y.K. qPCR quantification of sphaerodes mycoparasitica biotrophic mycoparasite interaction with *Fusarium graminearum*: In vitro and in planta assays. *Arch. Microbiol.* **2012**, *194*, 707–717. [[CrossRef](#)]
436. Gveroska, B.; Ziberoski, J. *Trichoderma harzianum* as a biocontrol agent against *Alternaria alternata* on tobacco. *Appl. Technol. Innov.* **2012**, *7*, 67–76. [[CrossRef](#)]
437. Matroudi, S.; Zamani, M.; Motallebi, M. Antagonistic effects of three species of *Trichoderma* sp. on *Sclerotinia sclerotiorum*, the causal agent of canola stem rot. *Egypt. Acad. J. Biol. Sci.* **2010**, *11*, 37–44.
438. De Meyer, G.; Bigirimana, J.; Elad, Y.; Höfte, M. Induced systemic resistance in *Trichoderma harzianum* T39 biocontrol of *Botrytis cinerea*. *Eur. J. Plant Pathol.* **1998**, *104*, 279–286. [[CrossRef](#)]
439. Herrera-Téllez, V.I.; Cruz-Olmedo, A.K.; Plasencia, J.; Gavilanes-Ruíz, M.; Arce-Cervantes, O.; Hernández-León, S.; Saucedo-García, M. The protective effect of *Trichoderma asperellum* on tomato plants against *Fusarium oxysporum* and *Botrytis cinerea* diseases involves inhibition of reactive oxygen species production. *Int. J. Mol. Sci.* **2019**, *20*, 2007. [[CrossRef](#)] [[PubMed](#)]
440. Cuervo-Parra, J.A.; Pérez España, V.H.; Zavala-González, E.A.; Peralta-Gil, M.; Aparicio Burgos, J.E.; Romero-Cortes, T. *Trichoderma asperellum* strains as potential biological control agents against *Fusarium verticillioides* and *Ustilago maydis* in maize. *Biocontrol. Sci. Technol.* **2022**, *32*, 624–647. [[CrossRef](#)]
441. Daniel, J.F.D.S.; Rodrigues Filho, E. Peptaibols of *Trichoderma*. *Nat. Prod. Rep.* **2007**, *24*, 1128–1141. [[CrossRef](#)]
442. Degenkolb, T.; Berg, A.; Gams, W.; Schlegel, B.; Gräfe, U. The occurrence of peptaibols and structurally related peptaibiotics in fungi and their mass spectrometric identification via diagnostic fragment ions. *J. Pept. Sci.* **2003**, *9*, 666–678. [[CrossRef](#)] [[PubMed](#)]
443. Shi, M.; Chen, L.; Wang, X.W.; Zhang, T.; Zhao, P.B.; Song, X.Y.; Sun, C.Y.; Chen, X.L.; Zhou, B.C.; Zhang, Y.Z. Antimicrobial peptaibols from *Trichoderma pseudokoningii* induce programmed cell death in plant fungal pathogens. *Microbiology* **2012**, *158*, 166–175. [[CrossRef](#)]
444. Zhang, Y.-Q.; Zhang, S.; Sun, M.-L.; Su, H.-N.; Li, H.-Y.; Liu, K.; Zhang, Y.-Z.; Chen, X.-L.; Cao, H.-Y.; Song, X.-Y. Antibacterial activity of peptaibols from *Trichoderma longibrachiatum* SMF2 against gram-negative *Xanthomonas oryzae* pv. *oryzae*, the causal agent of bacterial leaf blight on rice. *Front. Microbiol.* **2022**, *13*, 1034779.
445. Zhao, P.; Ren, A.; Dong, P.; Sheng, Y.; Li, D. Antimicrobial peptaibols, trichokonins, inhibit mycelial growth and sporulation and induce cell apoptosis in the pathogenic fungus *Botrytis cinerea*. *Appl. Biochem. Microbiol.* **2018**, *54*, 396–403. [[CrossRef](#)]
446. Otto, A.; Laub, A.; Wendt, L.; Porzel, A.; Schmidt, J.; Palfner, G.; Becerra, J.; Krüger, D.; Stadler, M.; Wessjohann, L.; et al. Chileno-peptins A and B, peptaibols from the Chilean *Sepedonium* aff. *chalcipori* KSH 883. *J. Nat. Prod.* **2016**, *79*, 929–938. [[CrossRef](#)]
447. Tamandegani, P.R.; Marik, T.; Zafari, D.; Balázs, D.; Vágvölgyi, C.; Szekeres, A.; Kredics, L. Changes in peptaibol production of *Trichoderma* species during in vitro antagonistic interactions with fungal plant pathogens. *Biomolecules* **2020**, *10*, 730. [[CrossRef](#)]
448. Luo, Y.; Zhang, D.D.; Dong, X.W.; Zhao, P.B.; Chen, L.L.; Song, X.Y.; Wang, X.J.; Chen, X.L.; Shi, M.; Zhang, Y.Z. Antimicrobial peptaibols induce defense responses and systemic resistance in tobacco against tobacco mosaic virus. *FEMS Microbiol. Lett.* **2010**, *313*, 120–126. [[CrossRef](#)]
449. Marik, T.; Tyagi, C.; Balázs, D.; Urbán, P.; Szepesi, Á.; Bakacsy, L.; Endre, G.; Rakk, D.; Szekeres, A.; Andersson, M.A.; et al. Structural diversity and bioactivities of peptaibol compounds from the Longibrachiatum clade of the filamentous fungal genus *Trichoderma*. *Front. Microbiol.* **2019**, *10*, 1434. [[CrossRef](#)] [[PubMed](#)]
450. Shores, M.; Yedidia, I.; Chet, I. Involvement of jasmonic acid/ethylene signaling pathway in the systemic resistance induced in cucumber by *Trichoderma asperellum* T203. *Phytopathology* **2005**, *95*, 76–84. [[CrossRef](#)]
451. Yedidia, I.; Benhamou, N.; Chet, I. Induction of defense responses in cucumber plants (*Cucumis sativus* L.) by the biocontrol agent *Trichoderma harzianum*. *Appl. Environ. Microbiol.* **1999**, *65*, 1061–1070. [[CrossRef](#)] [[PubMed](#)]
452. Huang, X.; Chen, L.; Ran, W.; Shen, Q.; Yang, X. *Trichoderma harzianum* strain SQR-T37 and its bio-organic fertilizer could control *Rhizoctonia solani* damping-off disease in cucumber seedlings mainly by the mycoparasitism. *Appl. Microbiol. Biotechnol.* **2011**, *91*, 741–755. [[CrossRef](#)] [[PubMed](#)]
453. Mendoza-Mendoza, A.; Zaid, R.; Lawry, R.; Hermosa, R.; Monte, E.; Horwitz, B.A.; Mukherjee, P.K. Molecular dialogues between *Trichoderma* and roots: Role of the fungal secretome. *Fungal Biol. Rev.* **2018**, *32*, 62–85. [[CrossRef](#)]

454. Brotman, Y.; Landau, U.; Cuadros-Inostroza, Á.; Takayuki, T.; Fernie, A.R.; Chet, I.; Viterbo, A.; Willmitzer, L. *Trichoderma*-plant root colonization: Escaping early plant defense responses and activation of the antioxidant machinery for saline stress tolerance. *PLoS Pathog.* **2013**, *9*, e1003221. [[CrossRef](#)]
455. Engelberth, J.; Koch, T.; Schüler, G.; Bachmann, N.; Rechtenbach, J.; Boland, W. Ion channel-forming alamethicin is a potent elicitor of volatile biosynthesis and tendrill coiling. Cross talk between jasmonate and salicylate signaling in lima bean. *Plant Physiol.* **2001**, *125*, 369–377. [[CrossRef](#)]
456. Rotblat, B.; Enshell-Seijffers, D.; Gershoni, J.M.; Schuster, S.; Avni, A. Identification of an essential component of the elicitation active site of the EIX protein elicitor. *Plant J.* **2002**, *32*, 1049–1055. [[CrossRef](#)]
457. Martinez, C.; Blanc, F.; le Claire, E.; Besnard, O.; Nicole, M.; Baccou, J.-C. Salicylic acid and ethylene pathways are differentially activated in melon cotyledons by active or heat-denatured cellulase from *Trichoderma longibrachiatum*. *Plant Physiol.* **2001**, *127*, 334–344. [[CrossRef](#)]
458. Morán-Diez, E.; Hermosa, R.; Ambrosino, P.; Cardoza, R.E.; Gutiérrez, S.; Lorito, M.; Monte, E. The ThPG1 endopolygalacturonase is required for the *Trichoderma harzianum*–plant beneficial interaction. *Mol. Plant Microbe Interact.* **2009**, *22*, 1021–1031. [[CrossRef](#)]
459. Hermosa, R.; Viterbo, A.; Chet, I.; Monte, E. Plant-beneficial effects of *Trichoderma* and of its genes. *Microbiology* **2012**, *158*, 17–25. [[CrossRef](#)] [[PubMed](#)]
460. Alonso-Ramírez, A.; Poveda, J.; Martín, I.; Hermosa, R.; Monte, E.; Nicolás, C. Salicylic acid prevents *Trichoderma harzianum* from entering the vascular system of roots. *Mol. Plant Pathol.* **2014**, *15*, 823–831. [[CrossRef](#)] [[PubMed](#)]
461. Ruocco, M.; Lanzuise, S.; Vinale, F.; Marra, R.; Turrà, D.; Woo, S.L.; Lorito, M. Identification of a new biocontrol gene in *Trichoderma atroviride*: The role of an ABC transporter membrane pump in the interaction with different plant-pathogenic fungi. *Mol. Plant Microbe Interact.* **2009**, *22*, 291–301. [[CrossRef](#)] [[PubMed](#)]
462. Masunaka, A.; Hyakumachi, M.; Takenaka, S. Plant growth-promoting fungus, *Trichoderma koningi* suppresses isoflavonoid phytoalexin vestitol production for colonization on/in the roots of *Lotus japonicus*. *Microbes Environ.* **2011**, *26*, 128–134. [[CrossRef](#)] [[PubMed](#)]
463. Wu, Y.; Li, J.; Yang, H.; Shin, H.-J. Fungal and mushroom hydrophobins: A review. *J. Mushroom* **2017**, *15*, 1–7. [[CrossRef](#)]
464. Dąbrowska, G.B.; Garstecka, Z.; Olewnik-Kruszkowska, E.; Szczepańska, G.; Ostrowski, M.; Mierek-Adamska, A. Comparative study of structural changes of polylactide and poly(ethylene terephthalate) in the presence of *Trichoderma viride*. *Int. J. Mol. Sci.* **2021**, *22*, 3491. [[CrossRef](#)]
465. Viterbo, A.; Harel, M.; Chet, I. Isolation of two aspartyl proteases from *Trichoderma asperellum* expressed during colonization of cucumber roots. *FEMS Microbiol. Lett.* **2004**, *238*, 151–158.
466. Saloheimo, M.; Paloheimo, M.; Hakola, S.; Pere, J.; Swanson, B.; Nyssönen, E.; Bhatia, A.; Ward, M.; Penttilä, M. Swollenin, a *Trichoderma reesei* protein with sequence similarity to the plant expansins, exhibits disruption activity on cellulosic materials. *Eur. J. Biochem.* **2002**, *269*, 4202–4211. [[CrossRef](#)]
467. Sánchez-Cruz, R.; Mehta, R.; Atriztán-Hernández, K.; Martínez-Villamil, O.; del Rayo Sánchez-Carbente, M.; Sánchez-Reyes, A.; Lira-Ruan, V.; González-Chávez, C.A.; Tabche-Barrera, M.L.; Bárcenas-Rodríguez, R.C.; et al. Effects on *Capsicum annuum* plants colonized with *Trichoderma atroviride* P. Karst strains genetically modified in *taswo1*, a gene coding for a protein with expansin-like activity. *Plants* **2021**, *10*, 1919. [[CrossRef](#)]
468. Macías-Rodríguez, L.; Guzmán-Gómez, A.; García-Juárez, P.; Contreras-Cornejo, H.A. *Trichoderma atroviride* promotes tomato development and alters the root exudation of carbohydrates, which stimulates fungal growth and the biocontrol of the phytopathogen *Phytophthora cinnamomi* in a tripartite interaction system. *FEMS Microbiol. Ecol.* **2018**, *94*, fyy137. [[CrossRef](#)]