International Journal of
Plant Biology

Review

Synergism or Antagonism: Do Arbuscular Mycorrhizal Fungi and Plant Growth-Promoting Rhizobacteria Work Together to Benefit Plants?

Noah Savastano * and Harsh Bais *

Department of Plant and Soil Sciences, University of Delaware, 357 AP Biopharma, 590 Avenue 1743, Newark, DE 19713, USA
* Correspondence: nsav@udel.edu (N.S.); hbais@udel.edu (H.B.)

Abstract: In agriculture, abiotic and biotic stress reduce yield by 51–82% and 10–16%, respectively. Applications of biological agents such as plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi (AMF) can improve plant growth. Applications of lone PGPR and AMF also help plants resist abiotic and biotic stressors. The reports for dual inoculation of AMF and PGPR to benefit plants and tackle stressors are largely unknown. It is speculated that PGPR colonization in plants enhances AMF infection during dual AMF and PGPR application, although increased AMF colonization does not always correlate with the increased benefits for the plant hosts. Further research is needed regarding molecular mechanisms of communication during dual inoculations, and dual-inoculation enhancement of induced systemic resistance under pathogen stress, to understand how dual inoculations can result in enhanced plant benefits. The influence of application timing of AMF and PGPR dual inoculations on mitigating abiotic and biotic stress is also not well understood. This review documents the factors that govern and modulate the dual application of AMF and PGPR for plant benefits against stress responses, specifically abiotic (drought) stress and stress from pathogen infection.

Keywords: microorganisms; plant beneficial microorganisms; abiotic stress; biotic stress; dual inoculation

Citation: Savastano, N.; Bais, H. Synergism or Antagonism: Do Arbuscular Mycorrhizal Fungi and Plant Growth-Promoting Rhizobacteria Work Together to Benefit Plants? *Int. J. Plant Biol.* **2024**, *15*, 944–958. https://doi.org/10.3390/ijpb15040067

Academic Editors: Ying Ma and Christopher Rensing

Received: 2 August 2024
Revised: 25 September 2024
Accepted: 27 September 2024
Published: 1 October 2024

1. Introduction

Each year, plant pathogens reduce global agricultural yields by 10–16% [1]. Additionally, abiotic stress decreases yield by 51–82% [2]. Agricultural yield loss from biotic and abiotic stress contributes to global food insecurity. Therefore, agricultural yield improvements are needed [1].

One approach to mitigating abiotic and biotic stress to improve yield is the application of biological agents. Biological agents have several advantages in comparison to more commonly used chemical agents, for plant pathogen control. Biological agent applications do not contaminate the environment or pose a risk to human health, unlike chemical pesticides. Also, biological agents increase plant growth under both ideal and stress conditions, improving crop yields [3].

Biological agents such as plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi (AMF) can improve plant pathogen resistance by acting antagonistically towards pathogens, mainly via competition and antimicrobial compound production [4]. Biological agents such as PGPR and AMF can also mitigate abiotic stress, specifically drought stress, by reducing cell damage, producing antioxidants, and improving water and nutrient uptake [5]. Additionally, dual inoculations of AMF and PGPR have enhanced plant benefits, compared to singular or no inoculation. PGPRs stimulate AMF colonization of plant roots, enhancing plant biomass and nutrient uptake [6–8]. Dual inoculations can also further enhance abiotic and biotic stress resistance, specifically by mitigating drought stress and improving plant pathogen defense [9–13].

However, there are several unknowns regarding the application of AMF and PGPR, both singularly and dually. Specifically, interactions between AMF, PGPR, and plants are not yet fully understood [14,15]. Also, it is known that the high diversity of the microbial community in the soil surrounding plant roots, the rhizosphere, is necessary for maintaining plant and soil health, both in general and under stress conditions [4,5]. However, a greater understanding is needed of how biological-control agent applications influence native soil microbes, and how the native microbial community affects the efficacy of biological agents [4].

This review will document several mechanisms of PGPR and AMF drought- and pathogen-stress mitigation, and the potential benefit of dual PGPR and AMF applications in mitigating plant stress.

2. Plant Growth-Promoting Rhizobacteria (PGPR)

Rhizobacteria colonize the area of soil surrounding plant roots known as the rhizosphere [16]. "Plant growth-promoting rhizobacteria" (PGPR) refers to 2–5% of rhizobacteria colonizing the rhizosphere that promote plant growth [16,17]. Plants and PGPR exchange chemical metabolites and create a symbiotic relationship with one another [18]. Within this relationship, PGPR promote plant growth by producing plant growth hormones including gibberellin and indole-3-acetic acid, to improve plant nutrient uptake. PGPR also improve nutrient availability and uptake by solubilizing insoluble phosphate, solubilizing iron via siderophore production and fixing atmospheric nitrogen. PGPR also mitigate plant pathogen stress, to promote plant growth in the presence of pathogens [16]. Additionally, PGPR aid plants in abiotic stress tolerance, such as tolerance to nutrient deficiency, heavy metals, salt, and drought [18]. While many studies have reported abiotic- and biotic-stress reduction via PGPR application, due to the vast number of plant and PGPR species, many species-specific PGPR–plant interactions under abiotic- and biotic-stress conditions are yet to be investigated. Some PGPR species' growth promotion is specific to plant species, cultivars, or genotypes. However, the specifications of PGPR–plant compatibility has not been well studied [16]. In addition, while previous studies have identified PGPR root colonization, they do not indicate which regions within the roots are colonized by PGPR. The specific site for PGPR root localization is key to deducing the interplay a PGPR colonization may have with AMF infection in plants.

2.1. Mechanisms of Mitigating Plant Drought Stress

2.1.1. Increased Proline Production

Reactive oxygen species (ROS) cause oxidative damage in plant cells, specifically affecting the DNA, lipids, and proteins within cells. Cellular damage from ROS occurs when plants experience abiotic stress, such as drought stress. Osmolytes such as proline act as ROS scavengers that neutralize ROS in plant cells. PGPR synthesize osmolytes, including proline, to mitigate oxidative damage from ROS during drought stress conditions [19]. Increased proline concentration correlates with the mitigation of drought stress in plants [20]. For cucumber (*Cucumis sativus* L.) under drought stress, inoculation with PGPR consortia including *Bacillus cereus* AR156, *Bacillus subtilis* SM21, and *Serratia* sp. XY21 increased proline content in leaves, as well as improving leaf chlorophyll content, and reduced wilt symptoms, compared to uninoculated plants [21]. Additionally, when maize (*Zea mays* L.) was exposed to drought stress, plants inoculated with PGPR *Bacillus* spp. produced more proline and had an increase in biomass compared to the control [22]. For *Thymus vulgaris*, *Santolina chamaecyparissus*, *Lavandula dentata*, and *Salvia officinalis* shrub species under drought conditions, PGPR inoculations improved nutrition and morphological traits in comparison to uninoculated plants. PGPR, especially *Bacillus* sp. and *Enterobacter* sp., also produced more proline to help remove free radicals from the plant when under drought stress. Bacterial inoculation increased proline content in *L. dentata* leaves [23]. Also, for wheat (*Triticum aestivum* L.) exposed to drought stress, *Bacillus megaterium* inoculation increased proline content, as well as improving relative water content, protein content, and chlorophyll a, b, and carotenoids [24].

2.1.2. Antioxidant Enzyme Production

PGPR have been found to regulate antioxidant enzyme activity in plants under drought stress. Antioxidant enzymes act as ROS scavengers, mitigating oxidative damage that normally occurs during drought stress. PGPR inoculants *Bacillus altitudinis* FD48 and *Bacillus methylotrophicus* RABA6 increased antioxidant enzyme activity, specifically superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and ascorbate reductase (APX), and mitigated drought stress for rice (*Oryza sativa*) exposed to drought conditions [25]. PGPR *B. megaterium* (MU2) increased SOD, POD, APX, CAT, and glutathione reductase (GR) activity and mitigated drought stress for wheat under drought conditions, in comparison to the control [24].

2.1.3. ABA Production, Regulating Stomatal Closure

PGPR inoculation increases abscisic acid (ABA) production in plants under drought conditions, resulting in a decrease in water loss and amelioration of drought stress. Increased ABA production from PGPR inoculation signals the plant to increase calcium levels in the cytosol of guard cells on plant leaves. Increased calcium levels enhance the rate of potassium and anion efflux out of the cell, causing water to exit the guard cell and turgor pressure to be lost. Reduction in turgor pressure triggers guard cells to close and decreases water loss via stomata [26]. PGPR inoculant *Azospirillum brasilense* Sp 245 enhanced ABA levels in *Arabidopsis thaliana* exposed to drought conditions compared to uninoculated plants, triggering the plants to close their stomata and conserve water. The PGPR inoculation and enhanced ABA production increased plant biomass and seed yield compared to the control [27]. Inoculants *Bacillus licheniformis* Rt4M10 and *Pseudomonas fluorescens* Rt6M10 also increased ABA production and minimized water loss for grapevine (*Vitis vinifera*) under water stress, leading to improved water content and turgidity [28]. Though previous studies found PGPR increase in ABA plant production to influence stomatal activity, they did not investigate other mechanisms of PGPR regulating pathways that control stomata opening and closing during drought stress [20].

2.1.4. Reduced Ethylene Overproduction

Plants respond differently to both biotic and abiotic stress, and ethylene as a signaling molecule plays a potential role in modulating root and shoot growth [29]. It is known that various PGPR mitigate ethylene production by synthesizing ACC deaminase (1-aminocyclopropane-1-carboxylate deaminase) to maintain plant growth [20,30]. During ethylene synthesis, ACC produced is a precursor of ethylene. ACC deaminase enzyme, produced by PGPR, deteriorates ACC, and therefore decreases ethylene production [29]. ACC deaminase production by *Enterobacter* sp., *Bacillus thuringiensis*, *Bacillus* sp., and *B. megaterium* inoculants mitigated drought stress for *T. vulgaris*, *S. chamaecyparissus*, *L. dentata*, and *S. officinalis* shrub species [23]. PGPR *B. licheniformis* inoculation produced ACC deaminase, and increased plant growth of pepper (*Capsicum annuum* L.) exposed to drought conditions in comparison to uninoculated plants [31]. Inoculants *Pseudomonas aeruginosa*, *Enterobacter cloacae*, *Achromobacter xylosoxidans* and *Leclercia adecarboxylata* increased shoot and root length for maize under drought stress, in comparison to uninoculated plants. It was suggested that ACC deaminase production decreased ethylene levels and led to increased plant growth [32].

2.1.5. Volatile Organic Compound (VOC) Production

PGPR produce volatile organic compounds (VOC) that induce stomatal closure, conserving water, and mitigating drought stress [33–35]. PGPR production of VOCs has been found to promote plant growth. Two PGPR strains produced VOC 2,3-butanediol and acetoin and increased growth in *Arabidopsis* in comparison to PGPR mutants that did not produce 2,3-butanediol and acetoin [35]. In drought conditions, PGPR *Pseudomonas chlororaphis* produced VOC 2,3-butanediol, which regulated stomatal closure and improved drought tolerance in *Arabidopsis* [33]. The VOC 2,3-butanediol, produced by PGPR, also induces nitric oxide and hydrogen peroxide production in plants. Nitric oxide and hydrogen peroxide both influence ABA signaling to close stomata and improve drought tolerance when plants are exposed to drought stress [34].

2.1.6. Extracellular Polymeric Substance (EPS) Production

Extracellular polymeric substances (EPS) are biopolymers that form the biofilm matrix [36]. EPS increase soil water retention and decrease soil drying rate [37]. For plants exposed to drought stress, EPS produced by PGPR help to create hydrophilic biofilms at the rhizosphere, improving drought tolerance [38]. When PGPR-inoculated maize was exposed to water stress, *Bacillus* spp. produced more EPS under drought conditions, improving water and nutrient uptake and increasing biomass in comparison to uninoculated plants [22]. PGPR production of EPS also mitigated drought stress for grapevine [38]. However, previous studies did not investigate EPS effect on plant physiology [39].

2.1.7. Summary

PGPR mitigate drought stress via several mechanisms. PGPR produce the osmolyte proline and regulate antioxidant enzyme activity, both of which act as ROS scavengers and neutralize ROS [19,24,25]. PGPR increase ABA production and production of VOCs to decrease water loss via stomata [26,34]. ACC deaminase production by PGPR reduces ethylene production to maintain plant growth under drought conditions [20,30]. Moreover, EPS production by PGPR produces hydrophilic biofilms surrounding plant roots, which improves drought tolerance [38]. Although several mechanisms of drought stress mitigation by PGPR have been identified, more efforts are needed to understand other mechanisms of improved drought tolerance by PGPR application. Examples of PGPR plant-growth promotion under drought stress are summarized in Table 1.

Table 1. Role of PGPR in plant growth enhancement and drought stress mitigation under drought stress.

PGPR	Plant	Response	Reference
Bacillus cereus AR156, *Bacillus subtilis* SM21, and *Serratia* sp. XY21	Cucumber	Increased leaf proline and chlorophyll content, decreased wilt symptoms	[21]
Bacillus spp.	Maize	Increased proline content, increased water and nutrient uptake, increased biomass	[22]
Enterobacter sp., *Bacillus thuringiensis*, *Bacillus* sp., and *Bacillus megaterium*	Shrub species	Improved nutrition, improved morphological traits, increased proline production, increased ACC deaminase production	[23]
Bacillus megaterium	Wheat	Increased proline content, relative water content, protein content, and chlorophyll a, b, carotenoids, and antioxidant enzyme activity	[24]
Bacillus altitudinis FD48 and *Bacillus methylotrophicus* RABA6	Rice	Increased antioxidant enzyme activity, mitigated drought stress	[25]
Azospirillum brasilense Sp 245	*Arabidopsis*	Increased ABA production, plant biomass, and seed yield	[27]
Bacillus licheniformis Rt4M10 and *Pseudomonas fluorescens* Rt6M10	Grapevine	Increased ABA production, water content, and turgidity	[28]
Bacillus licheniformis	Pepper	Increased ACC deaminase production and plant growth	[31]

Table 1. *Cont.*

PGPR	Plant	Response	Reference
Pseudomonas aeruginosa, *Enterobacter cloacae*, *Achromobacter xylosoxidans*, *Leclercia adecarboxylata*	Maize	Increased ACC deaminase production, shoot and root length	[32]
Bacillus subtilis GB03, *Bacillus amyloliquefaciens* IN937a	*Arabidopsis*	VOC 2,3-butanediol and acetoin production, increased plant growth	[35]
Pseudomonas chlororaphis	*Arabidopsis*	VOC 2,3-butanediol production, improved drought tolerance	[33]
Pseudomonas sp. S1, *Acinetobacter* sp. S2, *Pseudomonas* sp. S3, *Bacillus* sp. S4, *Delftia* sp. S5 and *Sphingobacterium* sp. S6	Grapevine	Increased plant growth, mitigated drought stress	[38]

2.2. PGPR and Plant Defense Response

In addition to improving plant abiotic stress resistance, PGPR inoculants enhance the ability of plants to resist stress from pathogens. Plants release root exudates that are metabolized by PGPR, while PGPR produce compounds to trigger ISR, and produce antifungal and antibacterial secondary metabolites that enhance pathogen resistance. When PGPR induce systemic resistance, parts of the plant not previously exposed to a given pathogen are protected from future infection via plant signaling pathways that mediate pathogen resistance [18]. When avocado (*Persea americana*) was inoculated with *B. subtilis*, the PGPR produced antifungal secondary metabolites that improved resistance to fungal pathogens. More *B. subtilis* was present on the rhizosphere of healthy avocado compared to avocado showing signs of fungal pathogen infection, implying that the PGPR presence improved fungal pathogen resistance [40]. PGPR can slow disease progression and prevent disease symptoms. Inoculant *B. subtilis* slowed powdery mildew disease progression in the beginning stages of development for strawberry (*Fragaria vesca* 'Elvira') [41]. Additionally, *B. subtilis* inoculation suppressed the *Rhizoctonia solani* pathogen and prevented wilting, a disease symptom, of cotton (*Gossypium hirsutum*) [42]. While previous studies have shown PGPR ability to slow and prevent disease, they did not fully investigate the mechanisms of pathogen resistance by PGPR [40].

2.3. PGPR Mitigating Plant Drought and Pathogen Stress

Since previous studies have identified PGPR mechanisms of pathogen and drought stress mitigation, it is thought that PGPR inoculation can improve abiotic- and biotic-stress resistance when plants are simultaneously exposed to drought stress and pathogen stress [43–45]. Additionally, PGPR application can indirectly improve abiotic- and biotic-stress resistance by increasing plant nutrient uptake and can further mitigate stress from simultaneous drought and pathogen stress [44,45]. However, few studies have been performed regarding PGPR mitigation of simultaneous drought and pathogen stress [44,45]. For bean (*Phaseolus vulgaris*), tomato (*Solanum lycopersicum*), and zucchini (*Cucurbita pepo* cv. Xara) inoculated with *Bacillus amyloliquefaciens* and under drought and pathogen stress, the PGPR induced an ISR response. Drought stress did not affect the ability of the PGPR to improve pathogen resistance [44]. Also, for rice under drought stress, PGPR *P. fluorescens* inoculation increased plant defense against six different pathogens by increasing abiotic- and biotic-defense enzyme production [45]. Although a few studies have previously demonstrated simultaneous pathogen and drought stress mitigation by PGPR, there is a lack of studies investigating species-specific interactions and mechanisms responsible for stress mitigation under dual abiotic and biotic stress conditions.

3. Arbuscular Mycorrhizal Fungi

Arbuscular mycorrhizal fungi are a type of endomycorrhizal fungi that colonize plant roots by entering the plant cell wall and moving into the plant cell membrane [46]. AMF form a mutually beneficial association with plants at the root level. AMF colonization enhances plant nutrient and water uptake, growth, and disease resistance. Meanwhile, AMF attain organic carbon from the plant, for their growth [47]. Mechanisms of plant growth promotion by AMF include hyphae improvement of nutrient and water uptake by plants, and production of glomalin to improve soil aggregation and nutrient availability. AMF also improve the plant defense response to pathogens. While some mechanisms of AMF plant growth promotion have been identified, more efforts are needed to understand enhancement of plant growth by AMF colonization [46]. AMF also improve plant resistance to abiotic stresses, including drought stress [47]. Previous studies found that the species AMF, associated with a certain plant species, influences the potential benefit of AMF colonization. However, studies identifying the ideal combination of AMF and plant species for enhanced plant benefit are yet to be performed [48].

3.1. AMF Mechanisms of Mitigating Plant Drought Stress

3.1.1. Hyphae Improve Plant Water Uptake

AMF hyphal networks increase surface area for water absorption to improve plant water uptake, which aids plants in drought resistance [49]. For trifoliate orange (*Poncirus trifoliata*) inoculated with *Funneliformis mosseae* and *Paraglomus occultum*, the water absorption rate of hyphae increased under drought conditions, indicating the significance of hyphal water uptake for plants under drought stress [50]. Moreover, *F. mosseae* and *Glomus constrictum* inoculation onto *Sophora davidii* under drought stress improved plant biomass, root length, and water use efficiency. The improved water use efficiency was attributed to AMF hyphae increasing plant water uptake [51].

3.1.2. Increased Reactive Oxygen Species (Hydrogen Peroxide) Efflux

AMF inoculation mitigates drought stress by increasing the efflux of hydrogen peroxide out of plant roots. Hydrogen peroxide presence, a reactive oxygen species, otherwise damages plants, via oxidative burst, when there is low hydrogen peroxide efflux. Two different studies of trifoliate orange under drought stress found that inoculation with *F. mosseae* enhanced drought stress tolerance by increasing hydrogen peroxide root efflux, resulting in increased biomass and plant growth promotion [52,53].

3.1.3. Increased Osmolyte Production

Similar to PGPR, AMF increase osmolyte levels that reduce oxidative stress from ROS during drought conditions. For shrubby horsetail (*Ephedra foliate*) under drought conditions, AMF *Glomus etunicatum*, *Rhizophagus irregularis*, and *F. mosseae* increased osmolyte production, mitigating oxidative damage from drought stress. The inoculated plants, as a result, had increased plant growth [54]. Also, when pistachio (*Pistacia vera*) was exposed to drought conditions, AMF *G. etunicatum* increased plant proline content, reducing oxidative damage and improving plant growth [55].

3.1.4. Increased Antioxidant Enzyme Production

AMF also increase antioxidant enzyme activity, similar to PGPR, to neutralize ROS and improve drought tolerance. *Rhizophagus intraradices* and *F. mosseae* AMF inoculants increased antioxidant enzyme activity for caucasian hackberry (*Celtis caucasica*) under drought conditions. The increased enzyme activity decreased hydrogen peroxide presence and correlated with an increase in plant growth [56]. *G. etunicatum* inoculant enhanced antioxidant enzymes of pistachio under drought conditions, increasing plant growth [55]. Additionally, AMF *G. etunicatum*, *R. irregularis*, and *F. mosseae* increased the activity of SOD, CAT, APX, and GR antioxidant enzymes for shrubby horsetail under drought stress, increasing plant growth [54].

3.1.5. Regulation of Aquaporins to Control Water Movement

Aquaporins are proteins that control water movement in cells. AMF regulate aquaporin activity in plants and in the fungus itself, to control water movement and improve drought tolerance [57,58]. The exposure to drought increased the expression of GintAQPF1 and GintAQPF2 aquaporin genes in *R. irregularis*, improving water transport to maize plants and increasing drought tolerance [58]. AMF *R. intraradices* inoculation also regulated aquaporin genes for maize under drought conditions, increasing plant growth [57]).

3.1.6. Summary

AMF reduce drought stress via multiple mechanisms. AMF production of hyphae increases the surface area for water and nutrient uptake [49]. AMF reduce oxidative stress by increasing hydrogen peroxide root efflux [52,53]. AMF also mitigate oxidative stress by producing osmolytes and increasing antioxidant enzyme activity to neutralize ROS during drought conditions [54,55]. Additionally, AMF regulate aquaporins to control water movement and reduce drought stress [57,58]. Studies identifying additional mechanisms of AMF drought stress mitigation are lacking. Examples of AMF plant growth promotion under drought conditions are summarized in Table 2.

Table 2. Role of AMF in plant growth enhancement and drought stress mitigation under drought stress.

AMF	Plant	Response	Reference
Funneliformis mosseae, Paraglomus occultum	Trifoliate orange	Increased water absorption rate via AMF hyphae	[50]
Funneliformis mosseae, Glomus constrictum	*Sophora davidii*	Increased plan biomass, root length, and water use efficiency via AMF hyphae	[51]
Funneliformis mosseae	Trifoliate orange	Increased hydrogen peroxide root efflux, biomass, and plant growth promotion	[52,53]
Glomus etunicatum, Rhizophagus irregularis, Funneliformis mosseae	Shrubby horsetail	Increased osmolyte production, antioxidant enzyme activity, and plant growth	[54]
Glomus etunicatum	Pistachio	Increased proline content, antioxidant enzyme production, and plant growth	[55]
Rhizophagus intraradices, Funneliformis mosseae	Caucasian hackberry	Increased antioxidant enzyme activity and plant growth	[56]
Rhizophagus irregularis	Maize	Increased expression of aquaporin genes, improved water transport	[58]
Rhizophagus intraradices	Maize	Improved aquaporin regulation, increased plant growth	[57]

3.2. AMF and Plant Defense Response

In addition to mitigating drought stress, AMF increase the plant defense response to pathogens. Improved plant nutrient uptake by AMF symbiosis enhances the ability of plants to resist disease. *Glomus* sp. colonization of tomato increased nitrogen, phosphorus, and potassium content and improved disease resistance to *Fusarium oxysporum* f. sp. *lycopersici* [59]. AMF *R. irregularis* provided nitrogen and carbon to inoculated soybean (*Glycine max*) infected with *Phytophthora sojae*, influencing the production of nitric oxide (NO), which signals pathogen resistance. The increased nitrogen and carbon uptake also enhanced the plant defense response [60]. AMF colonization on diseased plants also influences defense-related gene expression, mitigating disease. *Rhizoglomus irregulare* colonization upregulated defense-related gene expression in tomato and decreased tomato bushy stunt virus and tomato mosaic pathogen infection in young leaves [61]. *R. irregularis* increased jasmonic acid levels in soybean, which is involved in plant defense gene expression, mitigating *P. sojae* infection [60]. AMF colonization additionally enhances plant pathogen resistance by decreasing oxidative stress that occurs when ROS are produced during pathogen infection. *R. irregularis* decreased hydrogen peroxide buildup during *P. sojae* infection by increasing antioxidant enzyme activity, to improve pathogen resistance for soybean [60]. AMF *Glomus fasciculatum* colonization also decreased ROS presence in tomato, to enhance resistance to *F. oxysporum* f. sp. *lycopersici* [62]. While previous studies determined AMF plant pathogen mitigation, they did not deeply investigate AMF interactions with the host plant that resulted in improved pathogen resistance [60].

3.3. AMFs Improve Drought and Pathogen Resistance

AMF mitigation of abiotic and biotic stress similarly benefits plants affected by both drought stress and pathogen stress, simultaneously. Cowpea (*Vigna unguiculata*) infected with *Macrophomina phaseolina* (charcoal rot disease) and inoculated with *Glomus deserticola* and *Gigaspora gigantea* achieved normal growth under drought conditions [63]. AMF *Glomus monosporus* and *Glomus clarum* also reduced plant death and enhanced plant growth for date palm (*Phoenix dactylifera*) infected with *F. oxysporum* and exposed to drought stress [64]. Moreover, *Verticillium dahliae* pathogen had an especially negative effect on pepper under drought conditions, when not inoculated with *G. deserticola*, indicating the significance of AMF inoculation in mitigating abiotic and biotic stress [65]. However, few studies have previously investigated AMF reduction of simultaneous drought and pathogen stress and the mechanisms involved in abiotic and biotic stress reduction by AMF [63–65].

4. AMF and PGPR Dual Inoculation

4.1. Interactions of AMF and PGPR during Dual Inoculation

Although negative interactions are possible, dual inoculations with both PGPR and AMF most often have increased benefits for plants in comparison to singular or no inoculation. PGPR enhance plant growth when co-inoculated with AMF by stimulating AMF colonization, further benefiting the plant [6–8]. The inoculation of PGPR *B. subtilis* increased AMF *F. mosseae* colonization for rose-scented geranium (*Pelargonium graveolens*), increasing shoot biomass and nutrient uptake in comparison to singular or no inoculation [6]. *B. subtilis* also enhanced AMF *R. irregularis* colonization for onion (*Allium cepa*), increasing plant biomass and nutrient acquisition [7]. Additionally, *Bacillus amyloliquefaciens* increased the number of arbuscules and the glomalin production of AMF *Rhizophagus intraradices* when dually inoculated on winter wheat, indicating an increase in AMF biomass [8]. Notably, a meta-analysis found that although PGPR and AMF dual inoculation did have enhanced benefits, PGPR inoculation did not always increase AMF colonization, suggesting that other mechanisms may be responsible for the enhanced benefits of dual inoculation [15]. Few studies have investigated the interactions of specific AMF and PGPR species and the role of nutrients in plant–AMF–PGPR relationships [14,15]. Additionally, the influence of application timing on enhanced benefits of PGPR and AMF dual inoculations has yet to be studied.

4.2. Dual AMF and PGPR Inoculation Mitigates Plant Drought Stress

Dual inoculation of AMF and PGPR has been found to enhance drought stress tolerance for plants, compared to singular or no inoculation [9–11,13]. PGPR inoculation improves AMF growth and enhances the benefits of AMF inoculation for plants exposed to drought conditions. *Bacillus* sp. inoculation enhanced AMF *F. mosseae* and *R. irregularis* growth, mitigating drought stress for lettuce (*Lactuca sativa*) [13]. Dual inoculation also improves nutrient uptake, water uptake and photosynthetic activity, and reduces oxidative stress [9–11]. Co-inoculation of AMF, *Glomus versiforme*, and PGPR, *Bacillus methylotrophicus*, increased nitrogen, phosphorus, and potassium uptake and decreased oxidative stress by improving antioxidant enzyme activity for tobacco (*Nicotiana tabacum*). Dual inoculation also improved plant biomass and height [10]. Dual AMF and PGPR inoculation applied to date palm also improved nitrogen and phosphorus nutrient uptake and reduced oxidative stress. The dual inoculation additionally improved stomatal conductance, plant growth, and morphological traits, in comparison to singular or no inoculation. It was suggested that increased water and nutrient absorption by AMF hyphae improved plant nutrient uptake [9]. Dual inoculation of *R. irregularis* and *Bacillus thuringiensis* also increased water uptake for *Retama sphaerocarpa*, due to AMF hyphal water absorption [11]. Although previous studies found that dual AMF and PGPR mitigated drought stress, they did not investigate communication between plants, AMF, and PGPR at the molecular level, during drought conditions [12]. A summary of the mechanisms PGPR and AMF use independently to mitigate plant drought stress, and the benefits of dual PGPR and AMF applications for drought stress mitigation are shown in Figure 1.

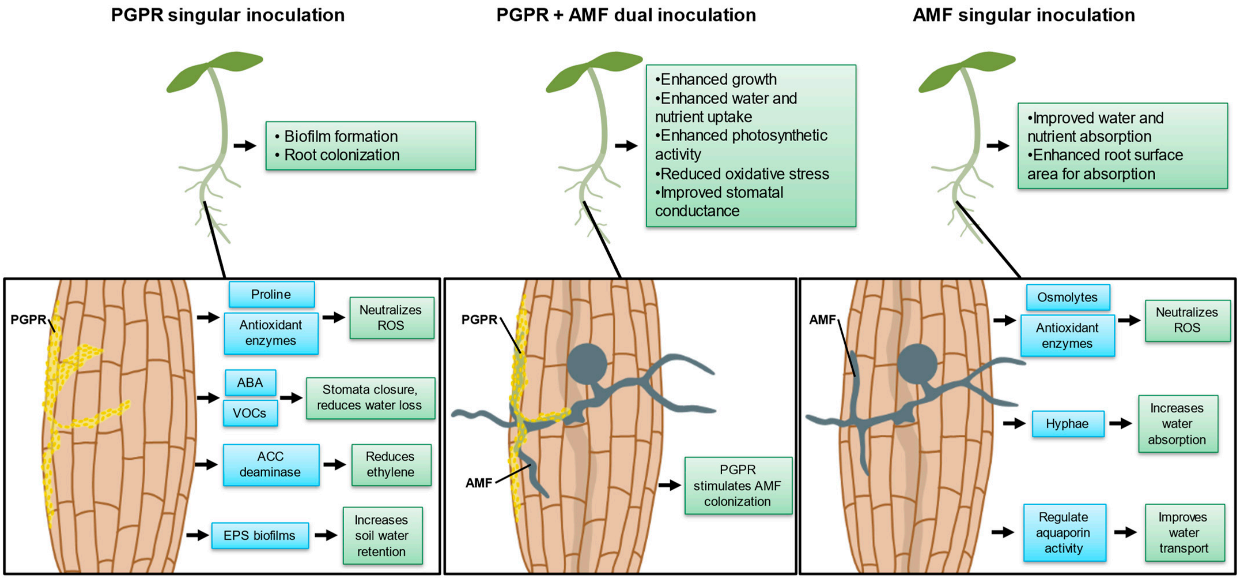

Figure 1. PGPR–AMF–plant interactions under drought stress. Schematic showing physiological and beneficial traits in plants inoculated with PGPR, AMF and a dual inoculation of PGPR and AMF.

4.3. AMF and PGPR Dual Inoculation Improves Pathogen Resistance

AMF and PGPR can provide enhanced benefits to plants under biotic stress when dually inoculated [12]. AMF and PGPR can both antagonistically toward plant pathogens and induce systemic resistance to improve plant defense [41]. AMF can compete with pathogens for resources to mitigate the negative impacts of the pathogen. AMF *Glomus* spp. increased competition with the white rot fungi pathogen (*Sclerotium rolfsii*), which improved pathogen defense for the common bean [66]. PGPR can also produce antipathogenic compounds to deter pathogens. PGPR *B. subtilis* produced antipathogenic compounds that improved white rot fungi disease resistance for the common bean [66]. The co-inoculation of AMF and PGPR can also enhance the activity of enzymes involved in pathogen defense more than using singular or no inoculation. Dual inoculation of *Glomus* spp. and *B. subtilis* enhanced peroxidase and polyphenyl oxidase (PPO) enzyme activity, which are both involved in plant pathogen defense [66]. Dual inoculation can also increase phosphorus uptake to improve plant growth during pathogen infection [66]. PGPR inoculation can increase the ability of AMF to improve phosphorus uptake for plants, by providing phosphorus in plant-available forms [67]. Although PGPR have been found to increase AMF colonization during dual inoculation to improve colonization benefits [6–8], PGPR inoculation does not always stimulate AMF colonization [66]. Also, when *R. irregularis* and *B. subtilis* were dually inoculated to enhance *Aspergillus niger* pathogen defense for lettuce, an increase in AMF colonization did not correlate with increased pathogen defense [67]. A lack of correlation indicates that other mechanisms enhance pathogen resistance during dual inoculation, although previous studies have not investigated how microbe–microbe interactions improve pathogen resistance and the benefit of dual AMF-PGPR application in agriculture [68]. Mechanisms of pathogen stress mitigation via individual PGPR and AMF applications, and the benefit of dual PGPR and AMF application in improving the plant pathogen defense response are summarized in Figure 2. Representative images of singular and dual PGPR and AMF root colonization are included in Figure 3.

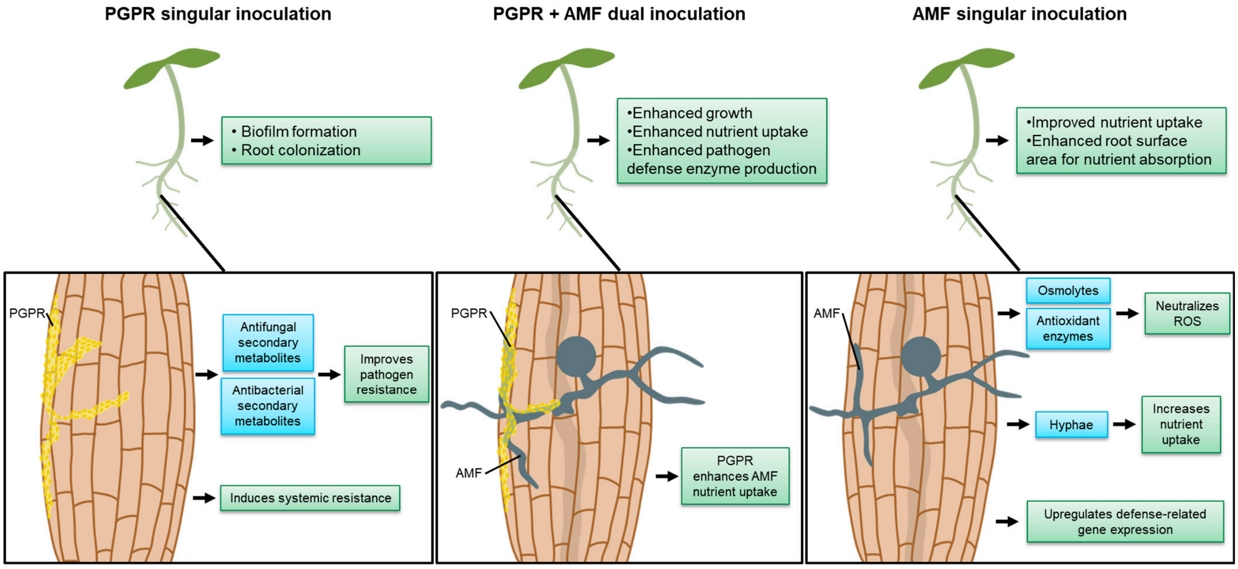

Figure 2. PGPR–AMF–plant interactions under biotic stress. Schematic showing physiological and beneficial traits in plants inoculated with PGPR and AMF and a dual inoculation of PGPR and AMF.

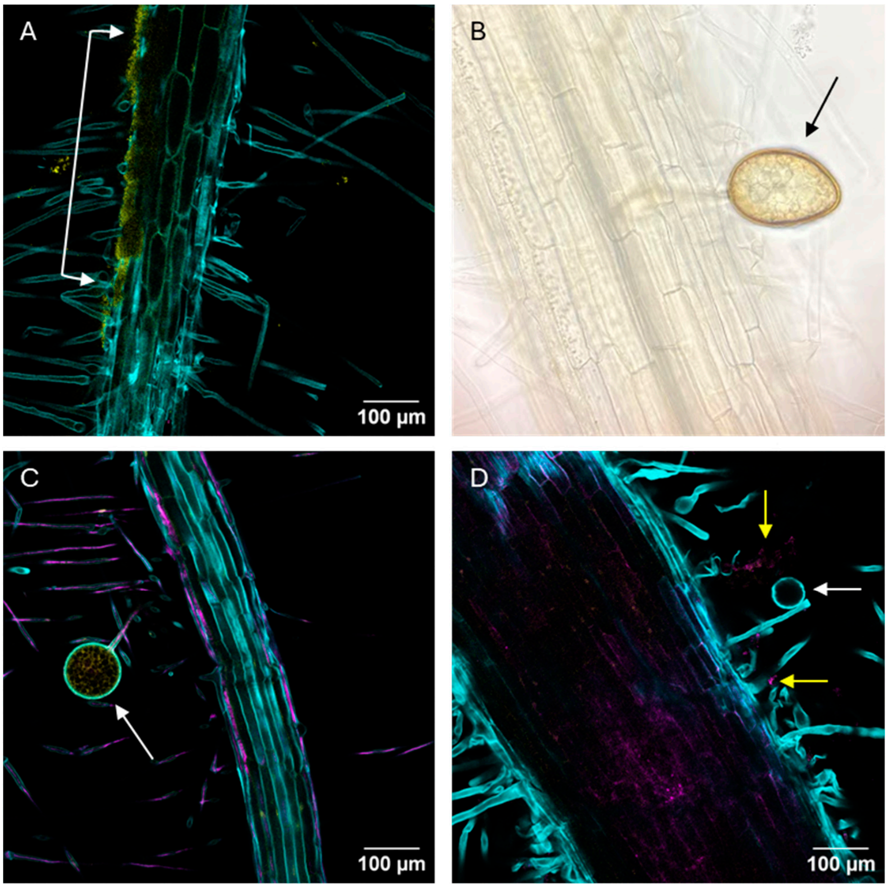

Figure 3. Representative micrographs depicting the single and dual colonization of PGPR (*B. subtilis*) and AMF (*R. irregularis*) on tomato roots. The arrow in (**A**) shows a fluorescent microscopy image of

B. subtilis root plane colonization. PGPR was stained with SYTO13 (yellow) fluorescent dye. (**B**) shows a phase image of an AMF spore on tomato root plane. (**C**) shows a fluorescent image of the single AMF colonization on tomato roots. AMF were stained with wheat germ agglutinin 594 (magenta) and calcofluor white (cyan) fluorescent dyes. (**D**) shows the dual inoculation of AMF and PGPR on tomato roots. The white arrow indicates an AMF spore, and yellow arrows show PGPR colonization on tomato roots.

5. Commercial AMF and PGPR Inoculums in the Agricultural Sector

Microorganisms were first applied agriculturally for plant benefit at the start of the 20th century, when rhizobial bacteria were applied to legume crops [69]. Availability of commercial PGPR and AMF inoculums arose more recently, in the 21st century [69]. Commercial PGPR products mainly include *Bacillus* and *Pseudomonas* bacterial strains [69]. Commercial AMF inoculums currently only include a select number of AMF strains in the *Glomeraceae* family [70]. Some of these products include AMF consortia of more than one AMF species [70]. However, products including multiple AMF strains may only enhance plant benefits if the strains included perform different beneficial effects [70]. While dual application can enhance plant benefits, few commercial products include both AMF and PGPR species [70]. Limitations to the commercial success of biological agents include short shelf life, variable benefits to plant growth, and a lack of understanding of how microbial inoculums may alter the native soil microbiota [46].

6. Conclusions

AMF and PGPR have several mechanisms for mitigating drought stress in plants. PGPR increase drought tolerance by increasing ABA production and producing VOCs to control stomata closure and decrease water loss. PGPR production of ACC deaminase also decreases ethylene production, to promote plant growth during drought conditions. PGPR also produce EPS to form hydrophilic biofilms and reduce drought stress. AMF colonization regulates aquaporin activity, to control water movement during drought conditions. AMF hyphae also increase plant water uptake. Both AMF and PGPR also reduce oxidative damage during drought by increasing osmolyte levels and increasing antioxidant enzyme activity. AMF also mitigate ROS damage by increasing the rate of hydrogen peroxide root efflux.

AMF and PGPR also promote pathogen defense. PGPR produce antipathogenic compounds and secondary metabolites, to reduce pathogen infection. PGPR additionally increase pathogen defense-related enzyme activity. PGPR also induce systemic resistance in plants. AMF promote plant health during pathogen infection by improving nutrient uptake. AMF also regulate defense-related gene expression. Additionally, AMF reduce oxidative stress during pathogen infection by increasing antioxidant enzyme activity. However, there has been little investigation into understanding the mechanisms of both PGPR and AMF in pathogen resistance.

PGPR and AMF dual inoculations promote abiotic- and biotic-stress tolerance in agriculture. Although previous studies found that dual inoculations increase water and nutrient uptake, enhance photosynthetic activity, and decrease oxidative stress in drought conditions, they did not fully investigate molecular-level communications of PGPR, AMF, and plants under drought stress. Dual inoculations also provide enhanced benefits under biotic stress. AMF compete with pathogens for resources to mitigate pathogen stress, while PGPR produce antipathogenic compounds to deter pathogens. Dual inoculation also increases phosphorus uptake, to improve plant health during pathogen infection. Additionally, co-inoculations enhance defense-related enzyme activity. D inoculation enhancement of ISR has been understudied.

PGPR can stimulate AMF colonization, to provide enhanced benefits during dual inoculation, although PGPR inoculation does not always result in increased AMF colonization, including during pathogen infection. Additionally, an increase in AMF colonization does not consistently correlate with improved pathogen defense, indicating that other mechanisms may enhance the benefits of dual AMF and PGPR associations. Though the enhanced plant benefits from AMF and PGPR dual inoculation have been studied previously, few studies identify mechanisms resulting in enhanced benefits.

There are several unknowns regarding interactions between PGPR, AMF, and plants. Mechanisms of pathogen defense, plant growth promotion, and the influence of species specificity are not well understood for singular PGPR or AMF inoculations. Additionally, the influence of species specificity, application timing, and nutrient availability on the enhanced benefits of dual AMF and PGPR inoculations is not well understood. More efforts are needed to understand the influence of dual inoculations on plants under abiotic and biotic stress, specifically molecular interactions under drought conditions and interactions that occur between microbes and plants, to improve pathogen resistance.

Author Contributions: Conceptualization, N.S. and H.B.; methodology, N.S. and H.B.; investigation, N.S. and H.B.; writing—original draft preparation, N.S. and H.B.; writing—review and editing, N.S. and H.B.; supervision, H.B. All authors have read and agreed to the published version of the manuscript.

Funding: The graduate assistantship to NS was funded through the UD-CANR support. The research was supported by the USDA-HATCH grant to HB. Microscopy was funded by grants from the NIH-NIGMS (P20 GM103446), the NIGMS (P20 GM139760) and the state of Delaware. Microscopy equipment was acquired with NIST (70NANB21H085).

Data Availability Statement: No new data were created or analyzed in this study. Data sharing is not applicable to this article. (Where no new data were created, or where data is unavailable due to privacy or ethical restrictions, a statement is still required. Please check if this statement is OK. Suggested Data Availability Statements are available in section "MDPI Research Data Policies" at https://www.mdpi.com/ethics.)

Acknowledgments: This manuscript is part of the thesis "The influence of plant growth-promoting rhizobacteria and arbuscular mycorrhizal fungi dual inoculation on tomato plants against abiotic stress regime" submitted to the University of Delaware by Noah Savastano for the fulfillment of a master's degree requirement. Microscopy access in the Bioimaging Facility at the Delaware Biotechnology Institute was supported by grants from the NIH-NIGMS (P20 GM103446), the NIGMS (P20 GM139760) and the state of Delaware. We thank Jeffrey Caplan and Tim Chaya in the Bio-Imaging Center for assistance with fluorescent microscopy imaging.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Chakraborty, S.; Newton, A.C. Climate Change, Plant Diseases and Food Security: An Overview. *Plant Pathol.* **2011**, *60*, 2–14. [CrossRef]
2. Oshunsanya, S.O.; Nwosu, N.J.; Li, Y. Abiotic Stress in Agricultural Crops Under Climatic Conditions. In *Sustainable Agriculture, Forest and Environmental Management*; Jhariya, M.K., Banerjee, A., Meena, R.S., Yadav, D.K., Eds.; Springer: Singapore, 2019; pp. 71–100. ISBN 978-981-13-6830-1.
3. Usta, C. Microorganisms in Biological Pest Control—A Review (Bacterial Toxin Application and Effect of Environmental Factors). In *Current Progress in Biological Research*; Silva-Opps, M., Ed.; InTech: London, UK, 2013; ISBN 978-953-51-1097-2.
4. de Faria, M.R.; Costa, L.S.A.S.; Chiaramonte, J.B.; Bettiol, W.; Mendes, R. The Rhizosphere Microbiome: Functions, Dynamics, and Role in Plant Protection. *Trop. Plant Pathol.* **2021**, *46*, 13–25. [CrossRef]
5. Vidal, C.; González, F.; Santander, C.; Pérez, R.; Gallardo, V.; Santos, C.; Aponte, H.; Ruiz, A.; Cornejo, P. Management of Rhizosphere Microbiota and Plant Production under Drought Stress: A Comprehensive Review. *Plants* **2022**, *11*, 2437. [CrossRef] [PubMed]
6. Alam, M.; Khaliq, A.; Sattar, A.; Shukla, R.S.; Anwar, M.; Dharni, S. Synergistic Effect of Arbuscular Mycorrhizal Fungi and Bacillus Subtilis on the Biomass and Essential Oil Yield of Rose-Scented Geranium (*Pelargonium Graveolens*). *Arch. Agron. Soil Sci.* **2011**, *57*, 889–898. [CrossRef]
7. Toro, M.; Azcon, R.; Barea, J. Improvement of Arbuscular Mycorrhiza Development by Inoculation of Soil with Phosphate-Solubilizing Rhizobacteria To Improve Rock Phosphate Bioavailability ((Sup32)P) and Nutrient Cycling. *Appl. Environ. Microbiol.* **1997**, *63*, 4408–4412. [CrossRef]
8. Wilkes, T.I.; Warner, D.J.; Edmonds-Brown, V.; Davies, K.G. Species-Specific Interactions of Bacillus Innocula and Arbuscular Mycorrhizal Fungi Symbiosis with Winter Wheat. *Microorganisms* **2020**, *8*, 1795. [CrossRef]

9. Anli, M.; Baslam, M.; Tahiri, A.; Raklami, A.; Symanczik, S.; Boutasknit, A.; Ait-El-Mokhtar, M.; Ben-Laouane, R.; Toubali, S.; Ait Rahou, Y.; et al. Biofertilizers as Strategies to Improve Photosynthetic Apparatus, Growth, and Drought Stress Tolerance in the Date Palm. *Front. Plant Sci.* **2020**, *11*, 516818. [CrossRef]
10. Begum, N.; Wang, L.; Ahmad, H.; Akhtar, K.; Roy, R.; Khan, M.I.; Zhao, T. Co-Inoculation of Arbuscular Mycorrhizal Fungi and the Plant Growth-Promoting Rhizobacteria Improve Growth and Photosynthesis in Tobacco Under Drought Stress by Up-Regulating Antioxidant and Mineral Nutrition Metabolism. *Microb. Ecol.* **2022**, *83*, 971–988. [CrossRef]
11. Marulanda, A.; Barea, J.M.; Azcón, R. An Indigenous Drought-Tolerant Strain of Glomus Intraradices Associated with a Native Bacterium Improves Water Transport and Root Development in Retama Sphaerocarpa. *Microb. Ecol.* **2006**, *52*, 670–678. [CrossRef]
12. Nanjundappa, A.; Bagyaraj, D.J.; Saxena, A.K.; Kumar, M.; Chakdar, H. Interaction between Arbuscular Mycorrhizal Fungi and *Bacillus* spp. in Soil Enhancing Growth of Crop Plants. *Fungal Biol. Biotechnol.* **2019**, *6*, 23. [CrossRef]
13. Vivas, A.; Marulanda, A.; Ruiz-Lozano, J.M.; Barea, J.M.; Azcón, R. Influence of a *Bacillus* sp. on Physiological Activities of Two Arbuscular Mycorrhizal Fungi and on Plant Responses to PEG-Induced Drought Stress. *Mycorrhiza* **2003**, *13*, 249–256. [CrossRef] [PubMed]
14. Gopal, S.; Chandrasekaran, M.; Shagol, C.; Kim, K.-Y.; Sa, T.-M. Spore Associated Bacteria (SAB) of Arbuscular Mycorrhizal Fungi (AMF) and Plant Growth Promoting Rhizobacteria (PGPR) Increase Nutrient Uptake and Plant Growth Under Stress Conditions. *Korean J. Soil Sci. Fertil.* **2012**, *45*, 582–592. [CrossRef]
15. Primieri, S.; Magnoli, S.M.; Koffel, T.; Stürmer, S.L.; Bever, J.D. Perennial, but Not Annual Legumes Synergistically Benefit from Infection with Arbuscular Mycorrhizal Fungi and Rhizobia: A Meta-analysis. *New Phytol.* **2022**, *233*, 505–514. [CrossRef] [PubMed]
16. Katiyar, D. Plant Growth Promoting Rhizobacteria-an Efficient Tool for Agriculture Promotion. *Adv. Plants Agric. Res.* **2016**, *4*, 426–434. [CrossRef]
17. Kloepper, J.W.; Schroth, M.N. Plant growth-promoting rhizobacteria on radishes. In Proceedings of the Station de Pathologie, 4th International Conference on Plant Pathogenic Bacteria, Tours, France, 27 August–2 September 1978; Végétale et Phyto-Bactériologie, Ed.; pp. 879–882.
18. Borriss, R. Use of Plant-Associated Bacillus Strains as Biofertilizers and Biocontrol Agents in Agriculture. In *Bacteria in Agrobiology: Plant Growth Responses*; Maheshwari, D.K., Ed.; Springer: Berlin/Heidelberg, Germany, 2011; pp. 41–76. ISBN 978-3-642-20331-2.
19. Das, K.; Roychoudhury, A. Reactive Oxygen Species (ROS) and Response of Antioxidants as ROS-Scavengers during Environmental Stress in Plants. *Front. Environ. Sci.* **2014**, *2*, 53. [CrossRef]
20. Sati, D.; Pande, V.; Pandey, S.C.; Samant, M. Recent Advances in PGPR and Molecular Mechanisms Involved in Drought Stress Resistance. *J. Soil Sci. Plant Nutr.* **2023**, *23*, 106–124. [CrossRef]
21. Wang, C.-J.; Yang, W.; Wang, C.; Gu, C.; Niu, D.-D.; Liu, H.-X.; Wang, Y.-P.; Guo, J.-H. Induction of Drought Tolerance in Cucumber Plants by a Consortium of Three Plant Growth-Promoting Rhizobacterium Strains. *PLoS ONE* **2012**, *7*, e52565. [CrossRef]
22. Vardharajula, S.; Zulfikar Ali, S.; Grover, M.; Reddy, G.; Bandi, V. Drought-Tolerant Plant Growth Promoting *Bacillus* spp.: Effect on Growth, Osmolytes, and Antioxidant Status of Maize under Drought Stress. *J. Plant Interact.* **2011**, *6*, 1–14. [CrossRef]
23. Armada, E.; Barea, J.-M.; Castillo, P.; Roldán, A.; Azcón, R. Characterization and Management of Autochthonous Bacterial Strains from Semiarid Soils of Spain and Their Interactions with Fermented Agrowastes to Improve Drought Tolerance in Native Shrub Species. *Appl. Soil Ecol.* **2015**, *96*, 306–318. [CrossRef]
24. Rashid, U.; Yasmin, H.; Hassan, M.N.; Naz, R.; Nosheen, A.; Sajjad, M.; Ilyas, N.; Keyani, R.; Jabeen, Z.; Mumtaz, S.; et al. Drought-Tolerant Bacillus Megaterium Isolated from Semi-Arid Conditions Induces Systemic Tolerance of Wheat under Drought Conditions. *Plant Cell Rep.* **2022**, *41*, 549–569. [CrossRef]
25. Narayanasamy, S.; Thangappan, S.; Uthandi, S. Plant Growth-Promoting *Bacillus* sp. Cahoots Moisture Stress Alleviation in Rice Genotypes by Triggering Antioxidant Defense System. *Microbiol. Res.* **2020**, *239*, 126518. [CrossRef] [PubMed]
26. Schroeder, J.I.; Kwak, J.M.; Allen, G.J. Guard Cell Abscisic Acid Signalling and Engineering Drought Hardiness in Plants. *Nature* **2001**, *410*, 327–330. [CrossRef] [PubMed]
27. Cohen, A.C.; Bottini, R.; Pontin, M.; Berli, F.J.; Moreno, D.; Boccanlandro, H.; Travaglia, C.N.; Piccoli, P.N. *Azospirillum Brasilense* Ameliorates the Response of *Arabidopsis Thaliana* to Drought Mainly via Enhancement of ABA Levels. *Physiol. Plant.* **2015**, *153*, 79–90. [CrossRef] [PubMed]
28. Salomon, M.V.; Bottini, R.; De Souza Filho, G.A.; Cohen, A.C.; Moreno, D.; Gil, M.; Piccoli, P. Bacteria Isolated from Roots and Rhizosphere of *Vitis Vinifera* Retard Water Losses, Induce Abscisic Acid Accumulation and Synthesis of Defense-related Terpenes in in Vitro Cultured Grapevine. *Physiol. Plant.* **2014**, *151*, 359–374. [CrossRef]
29. Vandana, U.K.; Singha, B.; Gulzar, A.B.M.; Mazumder, P.B. Molecular Mechanisms in Plant Growth Promoting Bacteria (PGPR) to Resist Environmental Stress in Plants. In *Molecular Aspects of Plant Beneficial Microbes in Agriculture*; Elsevier: Amsterdam, The Netherlands, 2020; pp. 221–233. ISBN 978-0-12-818469-1.
30. Ravanbakhsh, M.; Sasidharan, R.; Voesenek, L.A.C.J.; Kowalchuk, G.A.; Jousset, A. Microbial Modulation of Plant Ethylene Signaling: Ecological and Evolutionary Consequences. *Microbiome* **2018**, *6*, 52. [CrossRef]
31. Lim, J.-H.; Kim, S.-D. Induction of Drought Stress Resistance by Multi-Functional PGPR Bacillus Licheniformis K11 in Pepper. *Plant Pathol. J.* **2013**, *29*, 201–208. [CrossRef]
32. Danish, S.; Zafar-Ul-Hye, M.; Hussain, S.; Riaz, M.; Qayyum, M.F. Mitigation of Drought Stress in Maize through Inoculation with Drought Tolerant ACC Deaminase Containing PGPR under Axenic Conditions. *Pak. J. Bot.* **2020**, *52*, 49–60. [CrossRef]

33. Cho, S.M.; Kang, B.R.; Han, S.H.; Anderson, A.J.; Park, J.-Y.; Lee, Y.-H.; Cho, B.H.; Yang, K.-Y.; Ryu, C.-M.; Kim, Y.C. 2R,3R-Butanediol, a Bacterial Volatile Produced by *Pseudomonas Chlororaphis* O6, Is Involved in Induction of Systemic Tolerance to Drought in *Arabidopsis Thaliana*. *Mol. Plant-Microbe Interact.* **2008**, *21*, 1067–1075. [CrossRef]
34. Cho, S.-M.; Kim, Y.H.; Anderson, A.J.; Kim, Y.C. Nitric Oxide and Hydrogen Peroxide Production Are Involved in Systemic Drought Tolerance Induced by 2R,3R-Butanediol in Arabidopsis Thaliana. *Plant Pathol. J.* **2013**, *29*, 427–434. [CrossRef]
35. Ryu, C.-M.; Farag, M.A.; Hu, C.-H.; Reddy, M.S.; Wei, H.-X.; Paré, P.W.; Kloepper, J.W. Bacterial Volatiles Promote Growth in *Arabidopsis*. *Proc. Natl. Acad. Sci. USA* **2003**, *100*, 4927–4932. [CrossRef]
36. Flemming, H.-C.; Wingender, J. The Biofilm Matrix. *Nat. Rev. Microbiol.* **2010**, *8*, 623–633. [CrossRef] [PubMed]
37. Roberson, E.B.; Firestone, M.K. Relationship between Desiccation and Exopolysaccharide Production in a Soil *Pseudomonas* sp. *Appl. Environ. Microbiol.* **1992**, *58*, 1284–1291. [CrossRef] [PubMed]
38. Rolli, E.; Marasco, R.; Vigani, G.; Ettoumi, B.; Mapelli, F.; Deangelis, M.L.; Gandolfi, C.; Casati, E.; Previtali, F.; Gerbino, R.; et al. Improved Plant Resistance to Drought Is Promoted by the Root-associated Microbiome as a Water Stress-dependent Trait. *Environ. Microbiol.* **2015**, *17*, 316–331. [CrossRef] [PubMed]
39. Morcillo, R.; Manzanera, M. The Effects of Plant-Associated Bacterial Exopolysaccharides on Plant Abiotic Stress Tolerance. *Metabolites* **2021**, *11*, 337. [CrossRef] [PubMed]
40. Cazorla, F.M.; Romero, D.; Pérez-García, A.; Lugtenberg, B.J.J.; Vicente, A.D.; Bloemberg, G. Isolation and Characterization of Antagonistic Bacillus Subtilis Strains from the Avocado Rhizoplane Displaying Biocontrol Activity: Characterization of Antagonistic Bacillus. *J. Appl. Microbiol.* **2007**, *103*, 1950–1959. [CrossRef]
41. Lowe, A.; Rafferty-McArdle, S.M.; Cassells, A.C. Effects of AMF- and PGPR-Root Inoculation and a Foliar Chitosan Spray in Single and Combined Treatments on Powdery Mildew Disease in Strawberry. *Agric. Food Sci.* **2012**, *21*, 28–38. [CrossRef]
42. Medeiros, F.H.V.; Souza, R.M.; Medeiros, F.C.L.; Zhang, H.; Wheeler, T.; Payton, P.; Ferro, H.M.; Paré, P.W. Transcriptional Profiling in Cotton Associated with Bacillus Subtilis (UFLA285) Induced Biotic-Stress Tolerance. *Plant Soil* **2011**, *347*, 327–337. [CrossRef]
43. Nadeem, S.M.; Ahmad, M.; Zahir, Z.A.; Javaid, A.; Ashraf, M. The Role of Mycorrhizae and Plant Growth Promoting Rhizobacteria (PGPR) in Improving Crop Productivity under Stressful Environments. *Biotechnol. Adv.* **2014**, *32*, 429–448. [CrossRef]
44. Pertot, I.; Puopolo, G.; Hosni, T.; Pedrotti, L.; Jourdan, E.; Ongena, M. Limited Impact of Abiotic Stress on Surfactin Production in Planta and on Disease Resistance Induced by *Bacillus Amyloliquefaciens* S499 in Tomato and Bean. *FEMS Microbiol. Ecol.* **2013**, *86*, 505–519. [CrossRef]
45. Prathuangwong, S.; Chuaboon, W.; Chatnaparat, T.; Kladsuwan, L.; Shoorin, M.; Kasem, S. Induction of Disease and Drought Resistance in Rice by Pseudomonas Fluorescens SP007s. *CMU J. Nat. Sci. Spec. Issue Agric. Nat. Res.* **2012**, *11*, 45–55.
46. Sagar, A.; Rathore, P.; Ramteke, P.W.; Ramakrishna, W.; Reddy, M.S.; Pecoraro, L. Plant Growth Promoting Rhizobacteria, Arbuscular Mycorrhizal Fungi and Their Synergistic Interactions to Counteract the Negative Effects of Saline Soil on Agriculture: Key Macromolecules and Mechanisms. *Microorganisms* **2021**, *9*, 1491. [CrossRef] [PubMed]
47. Kumar, A.; Dames, J.F.; Gupta, A.; Sharma, S.; Gilbert, J.A.; Ahmad, P. Current Developments in Arbuscular Mycorrhizal Fungi Research and Its Role in Salinity Stress Alleviation: A Biotechnological Perspective. *Crit. Rev. Biotechnol.* **2015**, *35*, 461–474. [CrossRef] [PubMed]
48. Hage-Ahmed, K.; Rosner, K.; Steinkellner, S. Arbuscular Mycorrhizal Fungi and Their Response to Pesticides. *Pest Manag. Sci.* **2019**, *75*, 583–590. [CrossRef] [PubMed]
49. Pagano, M.C. Drought Stress and Mycorrhizal Plant. In *Use of Microbes for the Alleviation of Soil Stresses, Volume 1*; Miransari, M., Ed.; Springer: New York, NY, USA, 2014; pp. 97–110. ISBN 978-1-4614-9465-2.
50. Zhang, F.; Zou, Y.-N.; Wu, Q.-S. Quantitative Estimation of Water Uptake by Mycorrhizal Extraradical Hyphae in Citrus under Drought Stress. *Sci. Hortic.* **2018**, *229*, 132–136. [CrossRef]
51. Gong, M.; Tang, M.; Chen, H.; Zhang, Q.; Feng, X. Effects of Two Glomus Species on the Growth and Physiological Performance of Sophora Davidii Seedlings under Water Stress. *New For.* **2013**, *44*, 399–408. [CrossRef]
52. Huang, Y.-M.; Zou, Y.-N.; Wu, Q.-S. Alleviation of Drought Stress by Mycorrhizas Is Related to Increased Root H_2O_2 Efflux in Trifoliate Orange. *Sci. Rep.* **2017**, *7*, 42335. [CrossRef]
53. Zou, Y.-N.; Huang, Y.-M.; Wu, Q.-S.; He, X.-H. Mycorrhiza-Induced Lower Oxidative Burst Is Related with Higher Antioxidant Enzyme Activities, Net H_2O_2 Effluxes, and Ca^{2+} Influxes in Trifoliate Orange Roots under Drought Stress. *Mycorrhiza* **2015**, *25*, 143–152. [CrossRef]
54. Al-Arjani, A.-B.F.; Hashem, A.; Abd_Allah, E.F. Arbuscular Mycorrhizal Fungi Modulates Dynamics Tolerance Expression to Mitigate Drought Stress in Ephedra Foliata Boiss. *Saudi J. Biol. Sci.* **2020**, *27*, 380–394. [CrossRef]
55. Abbaspour, H.; Saeidi-Sar, S.; Afshari, H.; Abdel-Wahhab, M.A. Tolerance of Mycorrhiza Infected Pistachio (*Pistacia vera* L.) Seedling to Drought Stress under Glasshouse Conditions. *J. Plant Physiol.* **2012**, *169*, 704–709. [CrossRef]
56. Sepahvand, T.; Etemad, V.; Matinizade, M.; Shirvany, A. Symbiosis of AMF with Growth Modulation and Antioxidant Capacity of Caucasian Hackberry (*Celtis caucasica* L.) Seedlings under Drought Stress. *Cent. Asian J. Environ. Sci. Technol. Innov.* **2021**, *2*, 20–35. [CrossRef]
57. Bárzana, G.; Aroca, R.; Bienert, G.P.; Chaumont, F.; Ruiz-Lozano, J.M. New Insights into the Regulation of Aquaporins by the Arbuscular Mycorrhizal Symbiosis in Maize Plants Under Drought Stress and Possible Implications for Plant Performance. *Mol. Plant Microbe Interact.* **2014**, *27*, 349–363. [CrossRef] [PubMed]

58. Li, T.; Hu, Y.; Hao, Z.; Li, H.; Wang, Y.; Chen, B. First Cloning and Characterization of Two Functional Aquaporin Genes from an Arbuscular Mycorrhizal Fungus *Glomus Intraradices*. *New Phytol.* **2013**, *197*, 617–630. [CrossRef] [PubMed]
59. Kumari, S.M.P.; Prabina, B.J. Protection of Tomato, Lycopersicon Esculentum from Wilt Pathogen, *Fusarium Oxysporum* f.sp. *Lycopersici* by Arbuscular Mycorrhizal Fungi, *Glomus* sp. *Int. J. Curr. Microbiol. App. Sci.* **2019**, *8*, 1368–1378. [CrossRef]
60. Li, Y.; Liu, Z.; Hou, H.; Lei, H.; Zhu, X.; Li, X.; He, X.; Tian, C. Arbuscular Mycorrhizal Fungi-Enhanced Resistance against Phytophthora Sojae Infection on Soybean Leaves Is Mediated by a Network Involving Hydrogen Peroxide, Jasmonic Acid, and the Metabolism of Carbon and Nitrogen. *Acta Physiol. Plant* **2013**, *35*, 3465–3475. [CrossRef]
61. Khoshkhatti, N.; Eini, O.; Koolivand, D.; Pogiatzis, A.; Klironomos, J.N.; Pakpour, S. Differential Response of Mycorrhizal Plants to Tomato Bushy Stunt Virus and Tomato Mosaic Virus Infection. *Microorganisms* **2020**, *8*, 2038. [CrossRef] [PubMed]
62. Math, S.; Arya, S.; Sonawane, H.; Patil, V.; Chaskar, M. Arbuscular Mycorrhizal (*Glomus fasciculatum*) Fungi as a Plant Immunity Booster against Fungal Pathogen. *Curr. Agri. Res. J.* **2019**, *7*, 99–107. [CrossRef]
63. Oyewole, B.O.; Olawuyi, O.J.; Odebode, A.C.; Abiala, M.A. Influence of Arbuscular Mycorrhiza Fungi (AMF) on Drought Tolerance and Charcoal Rot Disease of Cowpea. *Biotechnol. Rep.* **2017**, *14*, 8–15. [CrossRef]
64. Meddich, A.; Ait El Mokhtar, M.; Bourzik, W.; Mitsui, T.; Baslam, M.; Hafidi, M. Optimizing Growth and Tolerance of Date Palm (*Phoenix dactylifera* L.) to Drought, Salinity, and Vascular Fusarium-Induced Wilt (*Fusarium oxysporum*) by Application of Arbuscular Mycorrhizal Fungi (AMF). In *Root Biology*; Giri, B., Prasad, R., Varma, A., Eds.; Soil Biology; Springer International Publishing: Cham, Switzerland, 2018; Volume 52, pp. 239–258. ISBN 978-3-319-75909-8.
65. Garmendia, I.; Goicoechea, N.; Aguirreolea, J. Moderate Drought Influences the Effect of Arbuscular Mycorrhizal Fungi as Biocontrol Agents against Verticillium-Induced Wilt in Pepper. *Mycorrhiza* **2005**, *15*, 345–356. [CrossRef]
66. Mohamed, I.; Eid, K.E.; Abbas, M.H.H.; Salem, A.A.; Ahmed, N.; Ali, M.; Shah, G.M.; Fang, C. Use of Plant Growth Promoting Rhizobacteria (PGPR) and Mycorrhizae to Improve the Growth and Nutrient Utilization of Common Bean in a Soil Infected with White Rot Fungi. *Ecotoxicol. Environ. Saf.* **2019**, *171*, 539–548. [CrossRef]
67. Kohler, J.; Caravaca, F.; Carrasco, L.; Roldán, A. Interactions between a Plant Growth-Promoting Rhizobacterium, an AM Fungus and a Phosphate-Solubilising Fungus in the Rhizosphere of *Lactuca sativa*. *Appl. Soil. Ecol.* **2007**, *35*, 480–487. [CrossRef]
68. Niu, B.; Wang, W.; Yuan, Z.; Sederoff, R.R.; Sederoff, H.; Chiang, V.L.; Borriss, R. Microbial Interactions Within Multiple-Strain Biological Control Agents Impact Soil-Borne Plant Disease. *Front. Microbiol.* **2020**, *11*, 585404. [CrossRef] [PubMed]
69. Backer, R.; Rokem, J.S.; Ilangumaran, G.; Lamont, J.; Praslickova, D.; Ricci, E.; Subramanian, S.; Smith, D.L. Plant Growth-Promoting Rhizobacteria: Context, Mechanisms of Action, and Roadmap to Commercialization of Biostimulants for Sustainable Agriculture. *Front. Plant Sci.* **2018**, *9*, 1473. [CrossRef] [PubMed]
70. Basiru, S.; Hijri, M. The Potential Applications of Commercial Arbuscular Mycorrhizal Fungal Inoculants and Their Ecological Consequences. *Microorganisms* **2022**, *10*, 1897. [CrossRef] [PubMed]