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Review

Introducing the Power of Plant Growth Promoting Microorganisms in Soilless Systems: A Promising Alternative for Sustainable Agriculture

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Abstract: Soilless systems, such as hydroponics and aquaponics, are gaining popularity as a sustainable alternative to traditional soil-based agriculture, aiming at maximizing plant productivity while minimizing resource use. Nonetheless, the absence of a soil matrix poses challenges that require precise management of nutrients, effective control of salinity stress, and proactive strategies to master disease management. Plant growth-promoting microorganisms (PGPM) have emerged as a promising solution to overcome these issues. Research demonstrated that *Bacillus*, *Pseudomonas*, and *Azospirillum* are the most extensively studied genera for their effectiveness as growth promoters, inducing changes in root architecture morphology. Furthermore, PGPM inoculation, either alone or in synergy, can reverse the effects of nutrient deficiency and salt stress. The genera *Pseudomonas* and *Trichoderma* were recognized for their solid antagonistic traits, which make them highly effective biocontrol agents in hydroponic systems. The latest findings indicate their ability to significantly reduce disease severity index (DSI) through mycoparasitism, antibiosis, and induced systemic resistance. In aquaponic systems, the inoculation with *Bacillus subtilis* and *Azospirillum brasilense* demonstrated increased dissolved oxygen, improving water quality parameters and benefiting plant and fish growth and metabolism. This review also establishes the interaction variability between PGPM and growing media, implying the specificity for determining inoculation strategies to maximize the productivity of soilless cultivation systems. These findings suggest that using PGPM in soil-free settings could significantly contribute to sustainable crop production, addressing the challenges of nutrient management, disease control, and salinity issues.

Keywords: PGPR; AMF; hydroponics; aquaponics; beneficial microorganisms; biological control agents

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1. Introduction

In the context of sustainability goals, it is essential to assess suitable instruments to facilitate the transition towards a resilient agricultural model that balances trade-offs between sustainability and intensification. The growing global population and food and water security concerns necessitate solutions prioritizing environmental sustainability and efficient production [1]. Farmers worldwide face significant challenges in meeting food production demands while mitigating the worsening state of the land caused by intensification. To ensure a sustainable food supply, there is a need to shift the focus from solely maximizing crop production to innovative and precise agriculture practices. Moreover, the predicted climate scenarios pose a considerable risk, particularly in regions heavily dependent on weather and seasonal changes. Nutrient-depleted soils, soil degradation, and water pollution are already a reality and are expected to worsen in the future [2]. Considering the trajectory of agriculture through the lenses of environmental sustainability and food security, soilless systems present an attractive option. These systems can reduce the negative impact of resource depletion and climate dependency, enabling the achievement of desired sustainability goals.

Soilless cultures can address numerous agricultural issues by improving water and nutrient use efficiency, promoting production sustainability, and adapting to the circular economy [3]. Consequently, soilless farming offers excellent potential for agriculture to achieve an environmentally friendly future and overcome challenges related to food security and quality control [4]. Growing crops in a medium other than soil is referred to as a soilless system, which includes hydroponics, a controlled environment agriculture based on substrate culture instead of soil for crop production [5,6]. Hydroponics allows for precise supply and regulation of the nutrient solution (NS) in the plants' rhizosphere, reducing problems related to soil pollution, enabling shorter crop cycles, and faster plant growth. Furthermore, this system is more efficient and accurate in regard to the use of water and fertilizers [6]. Hydroponics can be categorized into open and closed systems and varies in media used for crop growth, including liquid medium, organic (peat, rice husk, coco coir), and inorganic (rockwool, perlite, vermiculite, pumice) [7]. Soilless systems are known for their advantageous control over the microclimate, making them suitable for areas where agricultural production is typically challenging, such as degraded land, eroded soil, contaminated or acidified and salinized soil, and areas with a cold or deserted climate. This eliminates dependency on the season and geographical location [7]. In recent years, aquaponics, a type of hydroponics that combines fish and crop cultivation, has become an attractive form of precision farming [8]. This system utilizes fish effluent as the nutrient medium for plant growth, resulting in no or partial fertilization [9]. The coupled aquaponic system includes a unidirectional water flow from the fish to a hydroponic unit, which completes the cycle by returning to the fish tanks. In contrast, the decoupled system separates the aquaponic and hydroponic units, and the water flow does not return to the fish [10]. This type of farming is considered highly resource-efficient, providing control over essential elements required for crop and fish growth, and is not limited to growing seasons [11].

Meeting environmental and economic sustainability regulations has become increasingly important in modern agriculture. As a result, farmers are exploring alternative methods to increase production while minimizing negative environmental impacts. One promising solution is using Plant Growth Promoting Microorganisms (PGPM) in hydroponic systems. PGPM have been shown to improve plant performance and yield while addressing issues such as inadequate water quality that can cause soluble salt damage and nutrient imbalances. Moreover, salinity stress is a major challenge in hydroponic systems, negatively affecting plant growth and microbial populations. Halotolerant PGPM effectively enhance plant response to salinity stress [12]. Furthermore, using PGPM can help address plant protection challenges in soil-free systems. In contrast to soil-based agriculture, hydroponic systems create an environment that fosters pathogen proliferation. Therefore, integrated pest and disease management (IPDM) can be particularly challenging in hydroponic systems, and traditional chemical control methods may be detrimental to the overall system. Due to this, biological control methods such as PGPM are gaining attention as promising chemical control alternatives. While chemical control methods such as fungicides and nematicides are still commonly used in soil and soilless systems, their effectiveness, as well as availability of fungicides applicable to soilless cultures, is often limited [13]. Therefore, biological control methods such as PGPM offer a promising solution for sustainable pest and disease management in hydroponic systems.

The research continues developing more sustainable practices to solve three major issues mentioned above: plant growth improvement, diminishing salinity stress factors, and mastering disease control management. PGPM inoculants play a central role in sustainable agricultural management, as they can restore soil health and productivity. Furthermore, their potential applications extend beyond the traditional plant–microbe symbioses, making them a promising solution for low-input, sustainable agriculture [14].

Currently, a variety of microbial inoculants are available and have been proven effective by farmers and researchers, including Mycostop®, Prestop®, and EndoRoots Soluble®. The market for microbial inoculants has surpassed USD 1.5 billion and is projected to reach USD 4.5 billion in the next three years [15]. This growth suggests that microbial inoculants could become a practical and viable alternative to conventional fertilizers in the near future [16]. PGPM can be classified as growth promoters and biocontrollers, whose working mechanism acts beneficially directly and indirectly towards the host plants [17]. Further grouping defines as plant growth-promoting rhizobacteria (PGPR), plant growth-promoting fungi (PGPF), Arbuscular Mycorrhizal Fungi (AMF), Endophytes, and microalgae. Currently, there is a plethora of research on applying PGPM in soil. Thereby, this review broadly aims to provide a synthesis of up-to-date existing literature on the role of PGPM in hydroponics and aquaponics, specifically to identify the most tested genera and species related to their role as biofertilizers (i), salt-stress alleviators (ii), and biological control agents (BCA) (iii).

2. Categorization of Studies

A search was conducted in the Scopus database to gather the relevant literature on the use of PGPM in soilless cultivation systems, resulting in the selection of 46 papers published between 2003 and 2023. The selected literature focuses on the application of PGPM for various purposes, including plant growth promotion (i), biocontrol of plant diseases (ii), and improvement of salt-stress resistance (iii) (Figure 1) and associated genera studied for each purpose (Figure 2). The search used keywords such as "PGPR", "PGPF", "PGPM", "PGPB", "beneficial bacteria", "soilless system", "hydroponic", "aquaponic", "Arbuscular Mycorrhizal Fungi", "AMF", "endophyte", "endophytic", "Plant Growth", "biocontrol", "biological control agent", "avirulent", "salinity", "osmotic stress", "bioinoculant", and "biofertilizer", which were combined in various ways.

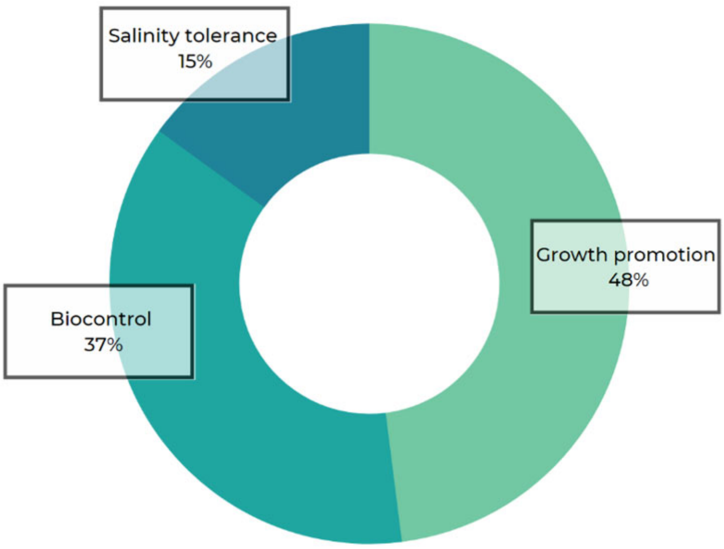

Figure 1. Percentage representation of studies divided by the aim of the study: growth promotion, biocontrol agents, salinity tolerance (data includes 46 papers in total).

The selection process included screening papers based on relevance in three stages: title and source (i), abstract (ii), and full text (iii). Only studies that focused on using plant-growth promoting microorganisms or "exogenous beneficial microorganisms" in growing media other than soil were considered relevant (Figure 3). The literature review followed a particularly suitable approach for examining provided evidence, clarifying main concepts and assumptions, and identifying knowledge gaps and key features related to beneficial microorganisms in soilless systems.

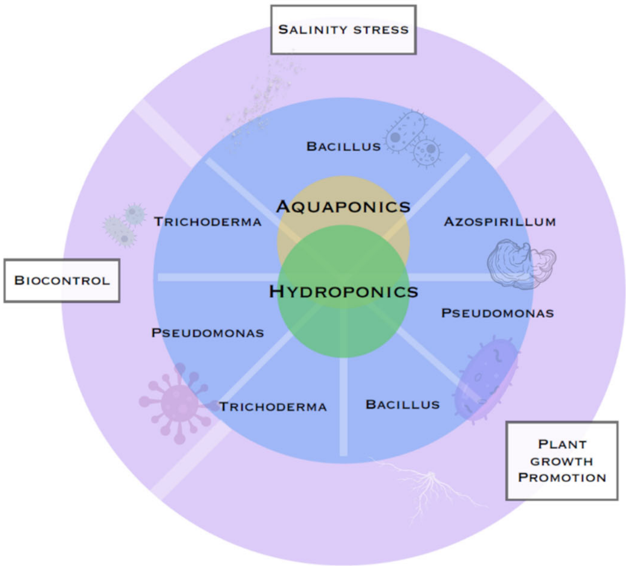

Figure 2. Most frequently tested genera as plant-growth promoters, biocontrollers, and salinity stress-alleviators in soilless systems.

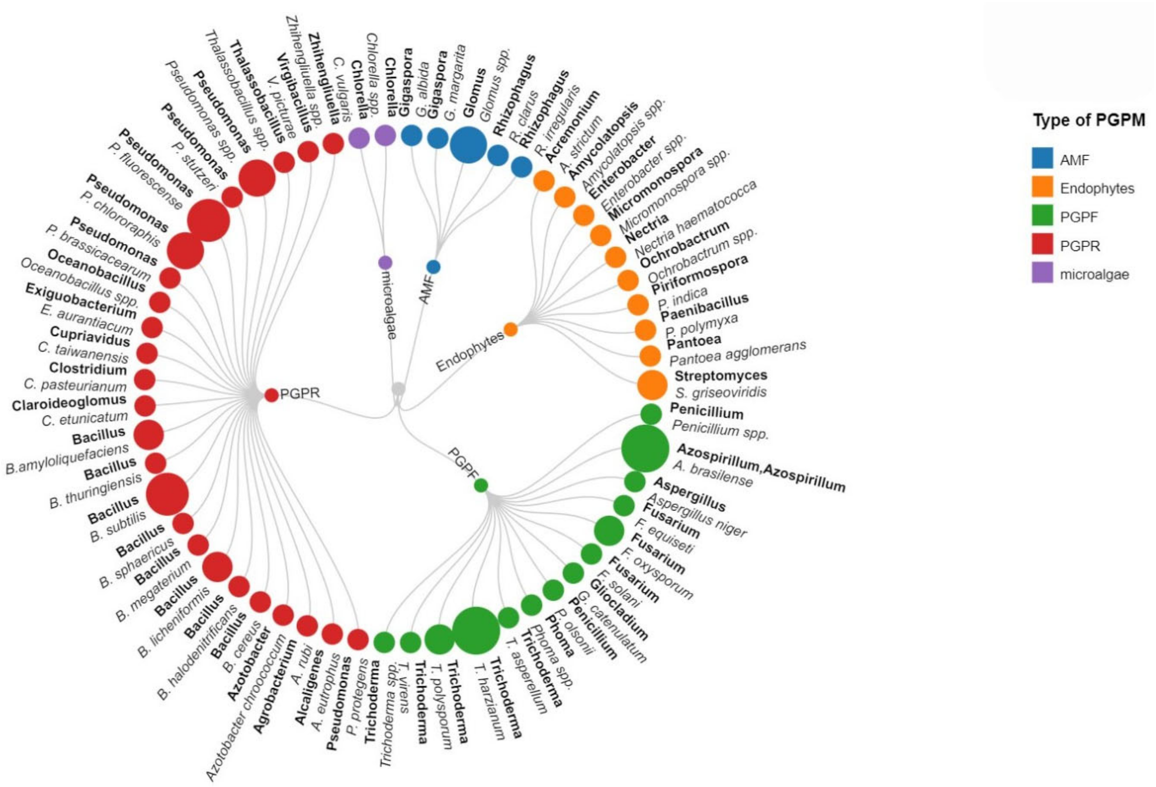

Figure 3. Visual representation of the taxonomic diversity and distribution of microorganisms as PGPM in soilless systems. The size of the circles indicates the numerical abundance of the microorganisms in the studies conducted.

3. PGPM as Plant-Promoting Growth Treatment and Facilitation of Nutrient Uptake

The potential of PGPM to enhance crop growth is widely recognized, as they can improve plant performance by promoting the mineral nutrient acquisition and converting unavailable nutrients into available forms [18]. *Bacillus*, *Pseudomonas*, and *Azospirillum* are the most extensively studied genera for their effectiveness as growth promoters in soilless cultivation systems (Figure 4), with species such as *Bacillus subtilis*, *Bacillus licheniformis*, *Pseudomonas fluorescens*, and *Azospirillum brasilense* among the most commonly tested (Table 1). These PGPM have demonstrated their ability to solubilize nutrients, which is particularly promising for increasing nutrient reuse efficiency in soilless systems, such as hydroponics and aquaponics [19]. In hydroponics, soil-related issues such as phosphate precipitation can also occur. In a study by Cerozi and Fitzsimmons [20], the introduction of various *Bacillus* spp. into aquaponics resulted in a significant increase in orthophosphate concentration and subsequent P accumulation. PGPM-mediated P solubilization is achieved by releasing mineral-dissolving compounds, such as organic acids, that can chelate cations bound to phosphate, converting it into a readily available form for crop uptake [21,22].

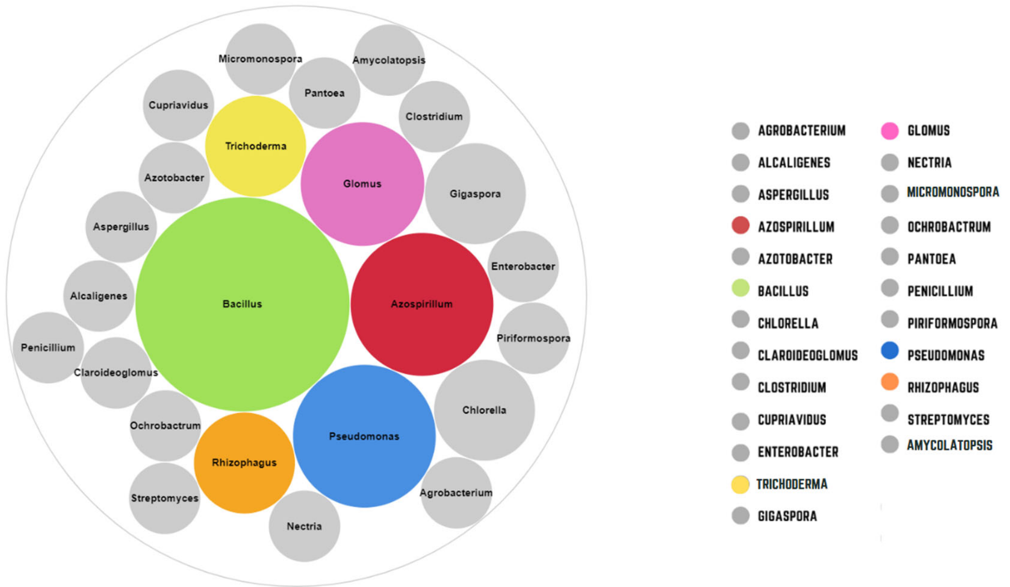

Figure 4. The most frequently studied genera for growth promotion purposes. It excludes the experiments of PGPM as BCA and crops with salinity stress. Colors are assigned to the most frequently tested genera (genera with lesser frequency in conducted studies are colorless).

PGPM can be applied in various ways (Tables 1–3). The most straightforward technique is to add a bio-inoculant directly to the NS or the growing medium. In aquaponic systems, the bio-inoculant can also be introduced into the biofilter or sump component [23]. An overview of PGPM addition to the aquaponic system, which combined the growth of seabass (*Lates calcarifer*) and basil, showed the alteration of root morphology of inoculated plants through auxin-IAA production by *Azospirillum brasilense*. This alteration extended the absorption area of water and minerals from the surrounding environment, resulting in improved physiological parameters of basil yield [24]. Similarly, in sweet basil, the impact was seen on the accumulation of sulfur (S) at the leaf level and increased iron (Fe) and phosphorus (P) concentration, doubling the plants' biomass [25]. Mia et al. [26] correlated banana plantlets' enhanced performance and the growth promoter's trait to improve nutrient accumulation, demonstrating the potential to decrease the amount of nitrogen (N) fertilizer and compensate for the N concentration in non-inoculated plants. Recent studies have shown that applying *A. brasilense* in consortium with *Trichoderma harzianum* enhanced leaf nutrient concentration, resulting in overall yield growth (by 10.91%) and better mass accumulation as dry root matter and chlorophyll index [27]. Similarly, Ribeiro et al. [28] pointed out that the consortium of *A. brasilense* with *B. subtilis* had a similar trend, increasing maize seedlings in hydroponics by 36% and enhancing parameters such as nutrient content and plant biomass.

Table 1. Application of PGPM in hydroponic systems for plant growth promotion. The table includes the crop where bio-inoculant was applied; the system (if described by the author) or the growing medium; species included in bio-inoculant, and their mechanism of action after introducing the crop.

Type of PGPM	Species	Mechanism	Crop	Application	System	Reference
PGPF	*Azospirillum brasilense*	auxin-IAA -> alter root morphology	basil	seedling	aquaponics, hydroponic gullies	[24]
PGPF	*Azospirillum brasilense*	elicited terpenoids and phenylpropanoids + synthesizing phytohormones	basil	NS	liquid medium	[25]
PGPF	*Pseudomonas* spp.	siderophore and IAA-like compounds production	apple *	NS	liquid medium	[29]
PGPF	*Trichoderma harzianum*, *Azospirillum brasilense*	increased leaf chlorophyll content, shoot and root growth, N acquisition	lettuce	foliar	NFT	[27]
Endophyte	*Ochrobactrum* spp., *Pantoea agglomerans*	secondary metabolite production, increasing iron uptake	cucumber **	seed coating	drip irrigation system, peat	[30]
Endophyte	*Nectria haematococca*	production of growth hormones, enhanced P content	mung bean	seeds	vermiculite	[31]
Endophyte	*Enterobacter* spp.	enhanced biomass, root growth, superoxide dismutase (SOD), catalase (CAT) content	pak choi	roots	liquid medium	[32]
Endophyte	*Streptomyces* spp., *Amycolatopsis* spp., *Micromonospora* spp.	IAA, NH3, Siderophore production, P solubilization	wheat	seedlings	liquid medium	[33]
AMF	*Glomus* spp., *Gigaspora margarita* EndoRoots Soluble®	improved photosynthesis, better supply of water and nutrients to the fruits	melon *	NS	cocopeat and perlite	[34]
AMF	*Rhizophagus irregularis* MycoPlant®	increased N, P content, seedling nutrient uptake, higher photosynthetic ability	tomato	NS	floating system	[35]
PGPR + AMF	*Azotobacter chroococcum*, *Azospirillum brasilense*, *Pseudomonas flourescens*, *Bacillus subtilis*, *Aspergillus niger*, *Glomus* spp.	increased efficiency of water translocation process, mineralization and solubilization of nutrients, production of phytohormones	tomato	roots	drip irrigation system, mix of rice straw charcoal, sand planting medium	[36]
PGPR, endophyte	*Bacillus cereus*, *Bacillus thuringiensis*, *Buttiauxella agrestis*	improved N content, extraction of nutrients from NS	banana	NS	floating system	[37]
endophyte + AMF	*Piriformospora indica*, *Rhizophagus clarus*, *Claroideoglomus etunicatum*, *Gigaspora albida*	affected mechanisms of absorption, translocation, and redistribution of nutrient	tomato ***	substrate	drip irrigation system, coconut fiber	[38]
AMF, Microalgae, PGPR	*Glomus* spp. EndoRoots Soluble®, *Chlorella* spp. Allgrow®, *Clostridium pasteurianum* Bio-one®	inoculation reduced effect of low nutrients supply	squash *	NS	perlite and cocopeat	[39]
PGPR(F)	*Bacillus subtilis*, *Trichoderma harzianum*	improved nutrient uptake	tomato	NS	perlite (open and close HS)	[40]

Table 1. *Cont.*

Type of PGPM	Species	Mechanism	Crop	Application	System	Reference
PGPR	*Bacillus megaterium*, *Agrobacterium rubi*, *Alcaligenes eutrophus*	mitigating effects on alkaline conditions	grapevine ***	NS	peat and perlite	[41]
PGPR	*Pseudomonas stutzeri*, *Cupriavidus taiwanensis*	production of antioxidant enzymes, higher root sulfide content, production of metal-binding peptides	rice ***	seedlings	liquid medium	[42]
PGPR	*Bacillus sphaericus*, *Azospirillum* spp.	increased chlorophyll content, N concentration, secretion of auxins, gibberellins and cytokinins	banana *	seedlings	liquid medium	[26]
PGPR	*Bacillus subtilis*, *Bacillus licheniformis*	solubilization of minerals, nitrogen fixation, enhanced concentrations of K, Na, P, and Zn	lettuce	NS	aquaponics, deep water culture	[23]
PGPR	*Pseudomonas chlororaphis*	upregulation of genes related to plant growth	lettuce **	roots	window farm, clay pellets	[43]
PGPR	*Bacillus subtilis* Sanolife® Pro-W	fish had higher activity of the digestive enzymes; production of endospores	mint	sump tank	recirculating aquaponics (*Nile tilapia*), HS-deep water culture	[44]
microalgae	*Chlorella vulgaris*	production of phytohormones-polyamines, betaines, brassinosteroids, and secretion of chelates; increased soluble solids (brix) and vitamin C	lettuce *	NS	liquid medium	[45]

* Experimental set of the system with reduced nutrient levels (N-free, Fe deficiency); ** crop with the presence of disease and pathogen (in lettuce—*Pythium ultimum*, in cucumber—Angular leaf spot disease); *** presence of stress factor in the system (grapevine—alkaline stress, rice—high As contents, tomato—high doses of K).

There is ample evidence of the ability of PGPM to promote plant growth under stress conditions while remaining metabolically active. For instance, Lee et al. [43] established a relationship between increased weight and length of lettuce and the upregulation of genes related to plant growth when *Pseudomonas chlororaphis* was introduced. Similarly, the beneficial traits of *Pseudomonas agglomerans*, when applied with *Bacillus pyrocinnia*, were attributed to P solubilization, ACC deaminase activity, and siderophore production [46]. Gao et al. [29] also reported a positive correlation between the output of pyoverdine (siderophore) in inoculated apple rootstocks and improved root surface area, length, and volume, leading to better plant-promoted features. Furthermore, Li et al. [47] reviewed key mechanisms and provided evidence of improved crop response to Fe deficiency. They discovered that *Pseudomonas*-induced changes in root architecture morphology enhanced primary root system function, including water and nutrient acquisition, positively affecting plant growth parameters. In addition, Thongnok et al. [42] highlighted the importance of beneficial microorganisms as growth promoters under stress conditions. The combined application of *P. stutzeri* with *Cupriavidus taiwanensis* showed increased tolerance of rice plants to As stress in a hydroponic system. In addition, these microorganisms exhibited strong antioxidant enzyme activities, IAA production and acted as an ethylene inhibitor. Therefore, the evidence suggests that PGPM can have an even higher impact on crop growth without stress conditions.

The genus *Bacillus* showed a range of responses in hydroponic experiments with the existing factor of salinity stress or N-free conditions. Mia et al. [26] determined that *Bacillus sphaericus* can be used as a viable alternative to commercial nitrogen fertilizers, as it has been shown to increase nitrogen concentration in both roots and leaves, resulting in improved production of primary, secondary, and tertiary roots, greater leaf area, and higher total chlorophyll content. *Bacillus subtilis* was determined to directly enhance nutrient acquisition in tomato plants, resulting in increased overall tomato yield (by 13.7%), consistent with the results of Kidoglu et al. [48], who reported augmented tomato yield by 36% when inoculated with *Bacillus* spp. [40]. In addition to its primary focus on growth-promoting features, *B. subtilis* was tested in a recirculating aquaponic system, where the cultivation of *Nile tilapia* fish and mint growth were combined. The bio-inoculant was introduced into the sump tank to assess water quality, as well as the performance and composition of fish and plants, the growth of the microbial community, and the food safety of the mint [44]. Satisfactory results showed higher plant length and protein contents in both fish and plants and higher moisture content in mint. In aquaponics, it is especially crucial to have water quality parameters maintained. When experimenting with PGPM, the researchers attempt to investigate the patterns of responses that contribute to those parameters. Khastini et al. [49] outlined improved water quality of a decoupled aquaponic system, including the effect on dissolved oxygen, which is crucial for milkfish respiration, and the nitrogenous waste produced by fish was significantly reduced. Moreover, this microbial consortia from several *Bacillus* spp., *Nitrosomonas*, *Nitrobacter*, *Lactobacillus casei*, and *Saccharomyces cerevisae* positively affected the spinach in the hydroponic unit, which produced more leaves and taller plants.

Several studies have extensively documented the successful utilization of a consortium of growth-promoting bacteria in conjunction with AMF. In addition to promoting nutrient uptake, this approach has also positively impacted photosynthesis [34,35]. For example, a positive correlation was observed between the overall yield growth of cherry tomatoes and the combination of mycorrhizal *Glomus* spp. with *Azotobacter chroococcum*, *A. brasilense*, *P. flourescens*, *B. subtilis*, *Aspergillus niger*. This synergistic inoculation increased the water translocation process and mineralization, the solubilization of nutrients, their improved absorption (N, P, K), and the production of phytohormones [36]. According to Dasgan et al. [39], using AMF with beneficial bacteria and microalgae has shown remarkable results. By enhancing mineral nutrient uptake, combining mycorrhiza (various *Glomus* spp.), *Clostridium pasteurianum*, and microalgae (numerous *Chlorella* spp.) improved crop response to low nutrient supply stress, resulting in a positive impact on fruit yield. Although controlled environment agriculture has many advantages, it is not always possible to create ideal conditions for crop growth. Sakamoto et al. [50] highlighted that even a slight deficiency in essential nutrient minerals could adversely affect the physiological parameters of plants. Hence, it expresses the attractiveness of bio-inoculants working in low nutrient-level systems. In a study by Cardoso et al. [38], a consortium of arbuscular mycorrhizal fungi and endophytes was successfully inoculated in tomato crops. The functional mechanisms of *Piriformospora indica*, *Rhizophagus clarus, Claroideoglomus etunicatum,* and *Gigaspora albida* were similar, facilitating the absorption, translocation, and redistribution of nutrients, even under conditions of excess or deficient levels of potassium.

Although the combination of AMF with other beneficial microorganisms has demonstrated significant results, single-type inoculation can also serve as a growth promoter. For example, *Rhizophagus irregularis*, when used in a hydroponic float system, altered the biometrical characteristics of tomato tissues, leading to immense total dry weight and root length, mainly by facilitating nutrient uptake with high N and P accumulation [35]. The authors also highlighted a positive correlation between higher doses of mycorrhiza and improved root development and plant biomass. In another study, Dere et al. [34] emphasized the crucial role of several species of *Glomus* and *Gigaspora* in acquiring P in systems with reduced nutrient levels. Besides promoting melon growth, biomass, and height, mycorrhizal inoculation enhanced plants' ability to photosynthesize efficiently, leading to better fruit development and increased total yield.

Endophytes have also been extensively tested in soilless systems for their ability to promote plant growth. They employ a similar growth-promoting mechanism to other

PGPM but establish a closer association with the plant by residing within the plant tissues and synthesizing metabolites immediately recognized by the plant [51]. Studies have shown that endophytic bacteria such as *Ochrobactrum* and *Pantoea agglomerans* can produce indole acetic acid (IAA), which stimulates root proliferation and facilitates iron uptake, increasing plant biomass, fresh fruit weight, and overall yield [30]. Thangavelu and Sulaiman [31] discovered that *Nectria haematococca*, an endophytic fungus, acted as a growth promoter by producing growth hormones, enhancing P content, and improving nutrient availability. Similarly, several species of *Streptomyces* and *Amycolatopsis*, belonging to the phylum *Actinobacteria*, were observed to promote plant growth in hydroponic systems by solubilizing P, producing IAA, siderophores, and NH3 [33]. Another endophytic bacterium, *Buttiauxella agrestis*, was determined to enhance nutrient extraction and promote banana growth when combined with *Bacillus* [37].

4. PGPM for Alleviation of Salinity Stress

The use of PGPM also has interesting implications in reversing the adverse effects of salt stress commonly observed in hydroponic systems. This stress negatively affects crop growth by creating an osmotic effect due to the accumulation of excess salt in the growing medium, leading to limitations in water uptake by roots [52]. Five studies investigated the efficacy of the genus *Bacillus* in promoting plant growth and mitigating the impact of salinity on crops (Table 2). Seifi et al. [53] determined that *B. subtilis* exhibited a halotolerant characteristic that reduces the synthesis of ethylene hormone, resulting in positive lettuce responses (both physiological and photosynthetic) to high electrical conductivity (EC) in irrigation water in a hydroponic system. Moncada et al. [54] demonstrated that Bacillus amyloliquefaciens reversed the reduction in lettuce biomass caused by salinity through changes in phytohormone content, antioxidant defense mechanisms, osmolyte production, and ACC deaminase activity. *Bacillus amyloliquefaciens* also showed potential as a stress alleviator by enhancing nutrient uptake and proline accumulation in crops subjected to saline conditions and inducing antioxidant levels [12]. Orhan [55] observed that *Bacillus* sp., when used in conjunction with the species *Zhihengliuella*, *Oceanobacillus*, and *Thalassobacillus*, demonstrated action mechanisms such as IAA production, N fixation, NH3 production, P solubilization, 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity, and accumulation of osmolytes. The trial also showed that the PGPM consortium, besides reducing salt stress, improved various wheat (*Triticum aestivum*) growth parameters, such as root and shoot length and total fresh weight.

Table 2. Use of PGPM for salt stress alleviation. The table includes the type of microbial inoculant with specified species, their action mechanism, and the type of substrate used for growing the crop in a hydroponic system. All studies listed in the table include the presence of the salinity problem.

Species	Mechanism	Crop	Growing Media	Reference
Bacillus subtillis	reduced synthesis of ethylene hormone; biophysics of the photosynthetic electron transport system	lettuce *	perlite	[53]
Bacillus subtillis FZB24® WG	resistance-inducing metabolites, production of lipopolysaccharides, enzymes, siderophores	tomato **	coco peat	[56]
Bacillus spp., *Zhihengliuella* spp., *Exiguobacterium aurantiacum*, *Virgibacillus picturae*, *Oceanobacillus* spp., *Thalassobacillus* spp.	IAA production, N fixation, NH3 production, P solubilization, ACC deaminase activity, accumulation of osmolytes	wheat	liquid medium	[55]
Pseudomonas fluorescens	upregulated protein expression levels, ACC deaminase	canola	liquid medium	[57]

Table 2. *Cont.*

Species	Mechanism	Crop	Growing Media	Reference
Bacillus amyloliquefaciens	enhanced nutrient uptake, stress alleviation, enhanced proline accumulation	rice	liquid medium	[12]
Bacillus amyloliquefaciens, *B. brevis*, *B. circulans*, *B. coagulans*, *B. firmus*, *B. halodenitrificans* *B. laterosporus*, *B. licheniformis*, *B. megaterium*, *B. mycoides*, *B. pasteurii*, *B. subtilis* TNC BactorrS13®	changes in phytohormone content, antioxidant defense, osmolyte production, ACC	lettuce	liquid medium	[54]
Penicillium olsonii	IAA production induced the catalase (CAT) and the superoxide dismutase (SOD) activities, enhanced chlorophyll, proline content	tobacco plants	liquid medium	[58]

* high EC; ** presence of fungal disease caused by *Pythium* and whitefly *Bemisia tabaci* in the crop.

5. PGPM as Biocontrol Agents

The potential of PGPR, PGPF, and endophytes as biocontrol agents against pathogens and diseases in soilless systems has been investigated in several studies conducted over the past twenty years. Among these studies, eight have focused on PGPR, eight on PGPF, and three on endophytes (Table 3). The shift from soil-based farming to hydroponic systems presents a significant risk of disease outbreaks caused by aquatic-adapted pathogens such as *Fusarium*, *Pythium*, and *Phytophthora* species. These pathogens can produce zoospores that rapidly infect new hosts in recirculating systems [59].

Table 3. Application of beneficial microorganisms in hydroponic systems for biocontrol purposes. The table includes the crop; the type of hydroponic system (if described by the author) or the substrate used for plant growth; species included in bio-inoculant, their mechanism of action, and the pathogen which caused plant disease in the crop.

BCA Species	Mechanism	Plant Disease	Crop	Application	System	Ref.
Trichoderma asperellum	mycoparasitism	*Cercospora hypha* (Leaf spot)	lettuce	foliar	NFT	[60]
Fusarium oxysporum	antagonistic activity, ISR, production of enzymes(chitinase)	*F. oxysporum f.* sp. *Cucumerinum* (wilt)	cucumber	roots	liquid medium	[61]
Trichoderma polysporum, *Trichoderma harzianum* Binab T®	competition for niche and nutrients, ISR	*Ralstonia solanacearum* (bacterial wilt)	tomato	seedlings	liquid medium	[62]
Fusarium equiseti, *Trichoderma* spp., *Penicillium* spp., *Phoma* sp.	inhibited the spore germination, ISR, direct antagonism	*Fusarium oxysporum* (crown and root rot)	tomato	seeds	rockwool, sub-irrigation system	[63]
Trichoderma polysporum, *Trichoderma harzianum*, *Streptomyces griseoviridis*	antagonistic activity	*Pythium aphanidermatum*, *Phytophthora cryptogea*	tomato	seedlings	pumice, peat; ebb and flow	[64]
Fusarium oxysporum	direct antagonism, ISR	*Curvularia lunata*, *Rhizoctonia solani*, *F. oxysporum f.* sp. *lactucae*	lettuce	roots	Deep Flow Technique	[65]
Pseudomonas sp., *Fusarium solani*. *Trichoderma* sp.	mycoparasitism, nutrient competition, ISR	*Phytophthora capsici* (crown rot)	zucchini	NS	peat	[13]

Table 3. *Cont.*

BCA Species	Mechanism	Plant Disease	Crop	Application	System	Ref.
Pseudomonas chlororaphis, *Trichoderma harzianum* RootShield® Drench, *Streptomyces griseoviridis* Mycostop®, *Gliocladium catenulatum* Prestop® WP, *Trichoderma virens* SoilGard®	outcompeting the pathogen for niche, nutrients; reduced spore germination	*Fusarium oxysporum* (root and stem rot)	cucumber	seeds	peat, rockwool	[66]
Pseudomonas spp., *Pseudomonas protegens*, *Pseudomonas brassicacearum*	production of antibiotics, phenazines, pyrrolnitrin, and/or pyoluteorin; ISR	*Agrobacterium rhizogenes* (hairy root disease)	tomato	roots	rockwool	[67]
Bacillus spp.	production of siderophores, protease, glucanase; ISR, induced SOD activity	*Pyricularia oryzae* (blast disease)	rice	NS	liquid medium	[68]
Pseudomonas chlororaphis, *Pseudomonas fluorescens*	antibiosis, ISR	*Fusarium oxysporum* (root rot)	tomato	seeds	liquid medium	[69]
Pseudomonas fluorescens	antagonistic activity-> reduction in severity of disease	*Pythium ultimum* (rot)	tomato	NS	NFT	[70]
Bacillus subtilis FZB24® WG	resistance-inducing metabolites, production of lipopolysaccharides, enzymes, siderophores	salinity, *Pythium*, *B. tabaci*	tomato	NS	coco peat	[56]
Pseudomonas chlororaphis	ISR, upregulation of protein involved in the jasmonic acid biosynthesis pathway	*Pythium ultimum*	lettuce	roots	window farm, clay pellets	[42]
Paenibacillus polymyxa	antagonistic activity, ISR	*Cercospora* sp. (leaf spot)	lettuce	NS	NFT	[71]
Acremonium strictum	antagonistic activity-> reduction in severity of disease	*Phytophthora cactorum*	strawberry	substrate	peat	[72]
Ochrobactrum spp., *Pantoea agglomerans*	colonization in all tissues provided sustainable antagonistic effects, ISR	angular leaf spot disease	cucumber	seed coating	drip irrigation system, peat	[30]

Applying biocontrol agents in soilless systems offers an advantage over soil-based cultivation, as hydroponic systems have limited space and volume, making the introduction of BCA into the rhizosphere easier. Conversely, in soil-based systems, it is challenging to apply beneficial microorganisms in sufficient concentrations to the lower parts of the root system [70]. Among the genera of microorganisms tested in hydroponic settings as biocontrol agents, *Pseudomonas*, *Fusarium*, and *Trichoderma* have been extensively studied (as shown in Figure 5) and have demonstrated high efficacy in reducing the severity of the disease index (SDI) and inducing defense mechanisms in plants. Beneficial microorganisms such as *Pseudomonas* and *Trichoderma*, in combination with *Fusarium solani*, have shown effective colonization of the rhizosphere and demonstrated mycoparasitism, antibiosis production, nutrient competition, and Induced Systemic Resistance (ISR) in plants. When tested in hydroponically grown zucchini, these species increased resistance to the phytopathogen *Phytophthora capsici*, resulting in better yields and reducing losses caused by crown rot. Hence, they exhibit great potential as biocontrol agents in hydroponic systems [13]. Similarly, *Acremonium strictum*, an endophytic species, has been determined to express antagonistic activity against *Phytophthora cactorum*, reducing disease pressure and severity (from 13.0 to 10.3%) in inoculated plants [72]. In soilless systems, biocontrol can act as a savior in case a pathogen such as *Phytophthora* enters the recirculating system, making control challenging to implement and necessitating the shutdown of the system for disinfection [73].

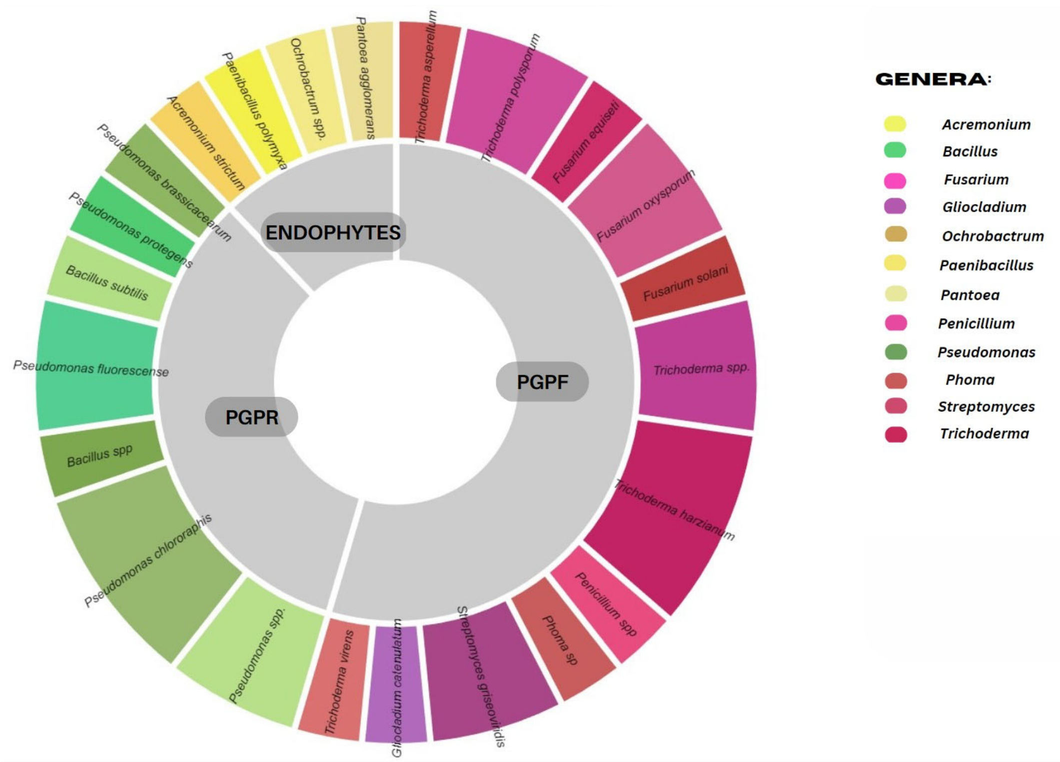

Figure 5. The most frequently studied species as BCA in soilless systems. The inner circle indicates three groups—PGPR, PGPF, and Endophytes. The outer ring represents species: Fungal—purple spectrum; bacteria—green; endophytic species—yellow. The size of each segment corresponds to the frequency of testing.

Trichoderma polysporum and *T. harzianum* exhibited strong antagonistic traits when applied in combination with the bacterium *Streptomyces griseoviridis* against *Phytophthora cryptogea* [64]. Inoculated in consortium with *Gliocladium catenulatum* and *Pseudomonas chlororaphis*, they outcompeted *Fusarium oxysporum* for niche and nutrients and successfully reduced its spore germination [66]. Mycoparasitism has also been determined to be an effective mechanism for inhibiting the pathogenic mycelial growth of *Cercospora hypha*, which causes foliar disease. All strains of *T. asperellum* tested in lettuce showed mycoparasitic ability by colonizing *C. hypha*, drilling holes in its mycelia, and reproducing conidia [60]. Additionally, in cucumbers attacked by *Fusarium*, the avirulent strain of the same genus (*F. oxysporum* CS-20) was determined to generate strong antagonistic activity, produce enzymes such as chitinase, and induce ISR, resulting in reduced DSI (from 61.67 to 41.67%) [61]. Direct antagonism was also observed between the beneficial *F. oxysporum* and *Curvularia lunata*, and *Rhizoctonia solani* present in lettuce crops, which was achieved by secreting spreading non-volatile inhibitory substances, promoting plant growth and accomplishing biocontrol goals [65]. In soilless systems, the inactivation of pathogens such as *F. oxysporum* is often treated with slow sand filtration, which does not eliminate them. Other physical methods, such as heat treatment or UV radiation, can also be used, but they affect the whole system, including the beneficial microbial community [74]. In hydroponic systems, treatments for *Fusarium* have shown low success rates, making biocontrol an attractive solution. Diverse species of *Trichoderma*, *Penicillium*, and *Phoma* have effectively reduced disease severity (from 59.3 to 3.7) and inhibited spore germination through direct [63]. In addition, *Pseudomonas chlororaphis* and *P. fluorescens* have been determined to reduce *Fusarium* root rot in tomatoes through antibiosis and ISR [69]. Said et al. [44] have also highlighted the potential of BCA-based solutions for aquaponics. Adding *B. subtilis* to the aquaponic system demonstrated that bacteria associated with seafood-borne infections, such as pathogenic *Bacillus cereus*, *Aeromonas hydrophila*, and *Acinetobacter baumannii*, were only detected in the fish from the control tank, while they were not detected in the tanks inoculated with *Bacillus*.

Pythium spp. is a common phytopathogen found in soilless systems and has been detected on roots in both the NFT system and NS, along with a significant number of aerobic bacteria [75]. Managing diseases caused by *Pythium* can be complex and costly, requiring chemical control. However, studies have shown that *Pseudomonas fluorescens* can alleviate tomato crop stress caused by *Pythium*, reducing the disease severity index from 3.9 to 1.2 [65]. Lee et al. [43] investigated the antagonistic interaction between *Pythium* as a pathogen and *Pseudomonas chlororaphis* as a biocontrol agent, demonstrating that *Pseudomonas* upregulates proteins involved in the jasmonic acid biosynthesis pathway and induces ISR. *Pseudomonas protegens* and *P. brassicacearum* were determined to be effective against hairy root disease caused by *Agrobacterium rhizogenes* in tomato crops by producing antibiotics such as phenazines, pyrrolnitrin, and pyoluteorin [67]. Despite being less common in soilless systems than fungal infections, the efficacy of *Pseudomonas* against bacterial infections has been confirmed [76].

According to Adhikari et al. [71], a single-type inoculation of the endophyte *Paenibacillus polymyxa* exhibited sufficient antagonistic activity, which resulted in the inhibition of mycelial growth of *Cercospora* and a subsequent reduction in leaf spot symptoms in lettuce. Meanwhile, Akköprü et al. [30] discovered that a mixed endophytic treatment of cucumber crops showed promising results in reducing Angular leaf spot disease. Various microorganisms, including *Ochrobactrum* spp. and *Pantoea agglomerans*, colonized all plant tissues, demonstrated sustainable antagonistic effects, and induced systemic resistance in plants.

Based on the findings of the studies mentioned above, it is possible to identify root rots as the most common type of disease in soilless cultivations. Biocontrollers with diverse mechanisms of action can enhance plant defense and combat pathogens, potentially reducing the need for fungicides and promoting sustainable practices. Beneficial microorganisms are advantageous as they compete for resources, produce antibiotics and cell-wall degrading enzymes, and induce systemic resistance in plants, making them stronger and less susceptible to pathogen attacks. This is critical for disease control in hydroponic crops. Furthermore, using beneficial microorganisms is simpler than current disease management practices, such as UV treatment, which can also eliminate beneficial microorganisms [74]. Ozonation, while effective, has downsides, such as reacting with iron chelates and making iron unavailable for plant uptake [77]. Therefore, beneficial microorganisms hold great promise for improving plant performance and biocontrol potential in soilless agriculture.

6. Substrate-PGPM Specificity

The ability of PGPM to colonize the rhizosphere is determined by factors such as the moisture-holding capacity, temperature, and electrical EC of the growing medium [77]. While most studies do not establish a clear correlation between the substrate and specific PGPM species, some assumptions can be made based on experiment results (Figure 6). Akkopru et al. [30] determined that the concentration of endophytes such as *Ochrobactrum* and *Pantoea agglomerans* decreased in plant organs and peat as a growing medium. In contrast, pumice was discovered to have better disease control potential and supported better colonization and antifungal activity of BCA such as *Trichoderma polysporum*, *T. harzianum*, and *Streptomyces griseoviridis*, particularly at the early stage of cultivation [66]. Gilardi et al. [13] reported that peat inoculation with a single or mixed BCA (*Pseudomonas* sp., *Fusarium solani*, *Trichoderma* sp.) failed to maintain a high population, rendering them ineffective at later stages. Gerrewey et al. [78] identified peat substrates lacking essential compounds for fungal colonization and growth. In contrast, reed straw-defibrated pure miscanthus and flax shives have been characterized as suitable substrates. The literature review indicates that AMF species have been tested in crops grown in various substrates, such as perlite, cocopeat, rice straw charcoal, and coconut fiber, except for one study by Roussis et al. [35], which used a liquid medium of a float system for tomato seedlings. Inoculating tomatoes grown in sawdust and coir substrate with the AMF inoculant containing *Glomus etunicatum*, *Paraglomus occultum*, *G. clarum*, and *G. mossea* did not result in expected growth promotion, possibly due to specific organic compounds such as phenolics and lignin in the growing media that hinder proper mycorrhizal structural development [79]. Kowalska et al. [80] suggested using rockwool as a suitable substrate for establishing an environment that promotes long-lasting symbiosis between mycorrhiza and plant roots.

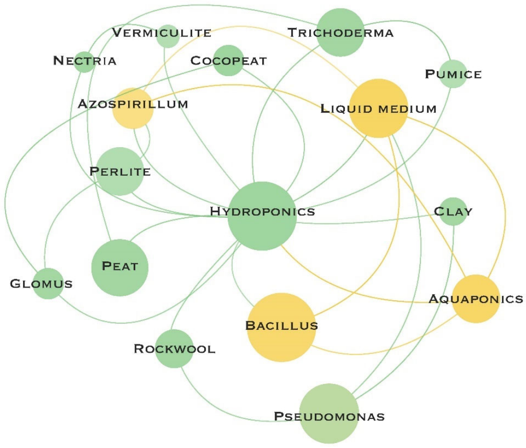

Figure 6. Network visualization of the most commonly studied genera in relation to the specific growing medium. Genera and substrates related to the hydroponic system are highlighted in green, while those related to aquaponics—in yellow. The larger circle size indicates more frequent testing.

According to Cela et al. [81], an increase in substrate moisture correlated with a decrease in the colonization of *Funneliformis mosseae* (AMF), suggesting a potential effect of bulk density on the colonization pattern. Previous studies have shown a direct relationship between the reduction in substrate total porosity and aeration space and an increase in the volume of water held by the substrate [82]. Gaur and Adholeya [83] investigated the effect of particle size of different substrates on AMF colonization. They determined that substrates with smaller particle sizes had better aeration, drainage, oxygen supply, and root growth, while those with bigger particles had fewer Inoculum Potential. Therefore, the correlation between substrate type and bio-inoculant species may not be straightforward, indicating a complex interaction between crop-specific environmental characteristics, the exogenous microbial community, and its colonization patterns.

7. Concluding Remarks and Future Implications

Due to projected population growth, arable land issues, and the effects of the climate crisis, there is a risk that agricultural production may not keep up with the increasing demand for food. One potential solution to this problem is soilless agriculture, which is expected to become more effective using beneficial microorganisms such as PGPM [84]. First, however, it is crucial to critically evaluate the evidence regarding the use of these microorganisms in hydroponic and aquaponic systems. By understanding the principle mechanism of rhizoengineers, we can see that improved crop performance results from genes in the microorganisms that are functionally related to promoting plant growth, altering root morphology, improving water translocation, and facilitating nutrient absorption and mineralization. Our search showed that the soilless observed trends in overall yield growth were similar to those reported in studies that employed PGPM in soil-based cropping systems; AMF inoculation in hydroponics, under reduced nutrient levels, increased the total yield by 49.54%, which is consistent with results obtained in soil cultivations (46–50% increase) [85]. In addition, endophytes were shown to increase total yield by 22.12%, just as demonstrated under limited-N soil conditions (31–39% increase) [86].

The features of a soilless system, such as a warm and humid environment and high nutrient availability, can lead to the growth of fungal phytopathogens such as *Phytophthora* spp. and *Pythium* spp., which can spread rapidly in recirculating water [87]. However, these systems also offer significant advantages, including controlled environmental conditions that can be optimized to support the growth of beneficial microorganisms, particularly those with biocontrol capabilities. When the biocontrol agent is taxonomically similar to the phytopathogen and shares similar properties, it can effectively suppress the growth of the pathogen [75]. Hydroponic systems also enhance the efficiency and longevity of biological control agents due to the lack of competition in the soil matrix [17]. Several studies have shown that pre-inoculation of plants with biocontrollers can mediate ISR, activated by signal molecules such as SA, JA, and ethylene, to control phytopathogens [61]. To maximize the suppressive traits of bioagents, a combination of species is recommended rather than single inoculations of each antagonistic microorganism. The efficacy of these agents against phytopathogens is due to their ability to produce antibiosis and siderophores and induce systemic resistance.

Incorporating knowledge of potential challenges in the biofertilization process is crucial for achieving beneficial outcomes. For instance, poor adaptation to a soilless system or crop specificity may lead to inadequate colonization of infection sites by BCA isolated from soil or a different crop [77]. The success of exogenous microorganism survival and beneficial environment establishment for both entities depend on their relationship with or competition against indigenous microorganisms [88]. However, all experiments indicate enhanced plant growth and parameters despite taxonomic shifts detected after PGPM introduction in soilless systems. Emblematic PGPM strains have been extensively characterized for owning plant-promoting features. Comprehending PGPM inoculation in both soil and soil-free production systems can offer sustainability-related benefits, including reduced fertilization levels and improved crop growth, and biocontrol protocols with reduced pesticide and fungicide application [89]. While research on the possible drawbacks of microbial inoculants in soilless settings is limited, a more thorough understanding of PGPM action mechanisms could reveal more effective fungal, bacterial, and mixture combinations to target growth promotion, salinity stress, or plant protection. Another aspect to consider is the plant host–PGPM specificity. Studies have shown decreased colonization density of PGPM at later harvest stages, suggesting the possibility of re-application of bio-inoculants in some cases.

As climate change and population growth continue to drive changes in global food demand, it is becoming increasingly clear that using PGPM-assisted practices can play a valuable role in creating a more resilient agricultural model. However, the key question remains: How to effectively implement these tools to design a sustainable and effective system? While there is already substantial evidence highlighting the potential of PGPM to reduce fertilizer inputs and establish effective plant protection strategies, further research is needed to fully understand how to maximize the benefits of sustainable farming without sacrificing yield.

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