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REVIEW ARTICLE

The fate of plant growth-promoting rhizobacteria in soilless agriculture: future perspectives

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Abstract

The application of plant growth-promoting rhizobacteria (PGPRs) can be an excellent and eco-friendly alternative to the use of chemical fertilizers. While PGPRs are often used in traditional agriculture to facilitate yield increases, their use in soilless agriculture has been limited. Soilless agriculture is growing in popularity among commercial farmers because it eliminates soil-borne problems, and the essential strategy is to keep the system as clean as possible. However, a new trend is the inclusion of PGPRs to enhance plant development. Despite the plethora of research that has been performed to date, there remains a huge knowledge gap that needs to be addressed to facilitate the commercialization of PGPRs for sustainable soilless agriculture. Hence, the development of proper strategies and additional research and trials are required. The present review provides an update on recent developments in the use of PGPRs in soilless agriculture, examining these bacteria from different perspectives in an attempt to generate critical discussion and aid in the understanding of the interaction between soilless agriculture and PGPRs.

Keywords Soil-free agriculture · Plant growth-promoting rhizobacteria (PGPR) · Biofertilizer · Microbial biotechnology

Introduction

The world's population is predicted to reach nearly 11 billion by 2100; thus, sustainable agriculture and food safety are foremost issues (United Nations 2017; Sambo et al. 2019; Chatterjee et al. 2020; Roberts et al. 2020). However, environmental pollution, increasing urbanization, and the gradual decrease in fertile soils have complicated these issues (Chen 2007). It has become a critical priority to develop safe agricultural products to support environmental and human health. One innovative solution to the challenges presented by infertile soil and the need for water conservation may be soilless agriculture (Sambo et al. 2019).

Soilless agriculture is growing in popularity among commercial farmers because it eliminates soil-borne problems. The global market for hydroponic systems (soilless agriculture) is estimated at $9.5 billion in 2020 and is predicted to reach $16.6 billion by 2025, growing at a five-year compound annual growth rate (CAGR) of 11.9% (Markets and markets 2020). The main strategy in soilless agriculture is to keep the system as clean as possible. However, a new trend is the inclusion of beneficial microorganisms to enhance the resistance to biotic and abiotic stress factors in the plants (Gül et al. 2013). Although beneficial microorganisms are found throughout the soil, they are most prevalent near plant roots in an area termed the rhizosphere (Ortega et al. 2017). PGPRs are mostly obtained from the soil. Bacteria from many genera, including *Alcaligenes*, *Agrobacterium*, *Azospirillum*, *Azotobacter*, *Arthrobacter*, *Bacillus*, *Bradyrhizobium*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Herbaspirillum*, *Klebsiella*, *Mesorhizobium*, *Micrococcus*, *Pseudomonas*, *Rhizobium*, *Rhodococcus*, and *Serratia*, can enhance plant growth (Azizoglu 2019). PGPRs can be divided into

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symbiotic bacteria and free-living rhizobacteria based on their interaction with plants. Symbiotic bacteria live within plant tissues and exchange metabolites with the host directly. However, free-living rhizobacteria live outside of plant tissues and promote plant growth (Gray and Smith 2005).

The mode of action of the effects of PGPRs on plants can be direct or indirect. Direct mechanisms include biofertilization (nitrogen (N_2) fixation, production of plant hormones and siderophores (SDs), phosphorus (P) solubilization, etc.), root growth stimulation, rhizoremediation, and the control of plant stress (Vejan et al. 2016). Additionally, PGPRs produce metabolites, such as indole-3-acetic acid (IAA), 1-aminocyclopropane-1-carboxylate-deaminase (ACC-deaminase), phosphate solubilizing enzyme (PSE), and SDs (Jouzani et al. 2017; Azizoglu 2019). They can also indirectly enhance plant growth by reducing the detrimental effects of phytopathogens through induced systemic resistance (ISR) and the production of antimicrobial compounds, such as bacteriocin, zwittermicin, fengycin, chitinase, and cell wall-degrading enzymes (Fig. 1) (Vessey 2003; Raddadi et al. 2007; Egamberdieva and Lugtenberg 2014; Vejan et al. 2016; Jouzani et al. 2017; Azizoglu 2019). Although several studies have indicated that PGPRs can be successfully used in soilless agriculture (Gül et al. 2008, 2013; Kıdoğlu et al. 2009; Baset Mia et al. 2010; Gul et al. 2012; Zafar et al. 2012), it remains unknown whether they will adapt to a different environment from their natural habitat when used in this manner (Fig. 2).

In this review, we focus on the future of PGPRs in soilless agriculture, placing their use into perspective with other views to discuss and evaluate the recent advances in the biotechnological applications of these rhizobacteria.

Overview of soilless agriculture and recent advances

Soilless agriculture is a method based on the cultivation of plants in substrates other than the soil (Savvas and Gruda 2018) and dates back to ancient times. The cultivation of plants in pots placed on the soil surface has been attempted at various times throughout the ages. For instance, Egyptians utilized this method of plant cultivation 4000 years ago, and the murals found in the temple of Deir el-Bahari are known as the first documented evidence of plants being grown in pots (Raviv et al. 2019).

The use of smart applications in agriculture has recently become widespread. Many technological tools have also been implemented, such as satellite controls, global system for mobile communication (GSM) operators, sensors, mini weather stations, drones for aerial monitoring, and unmanned aerial vehicles. The techniques involving these applications and tools are termed "*innovation techniques*". Thanks to these techniques, agricultural productivity is

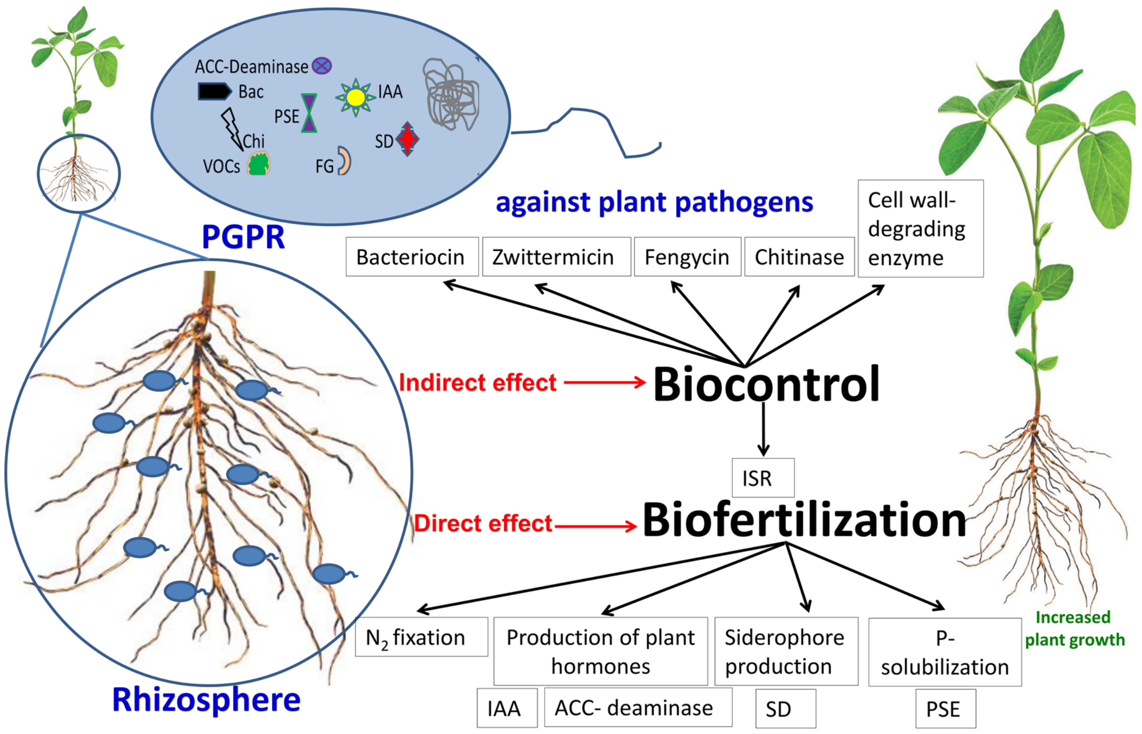

Fig. 1 Mechanism of action of PGPR. *ACC* ACC-deaminase, *Bac* bacteriocin, *Chi* chitinase, *SD* siderophore, *FG* fengycin, *ISR* induced systemic resistance, *IAA* indole-3-acetic acid, *PSE* phosphate solubilization enzymes, *VOCs* volatile compounds, modified from Jouzani et al. (2017) and Azizoglu (2019)

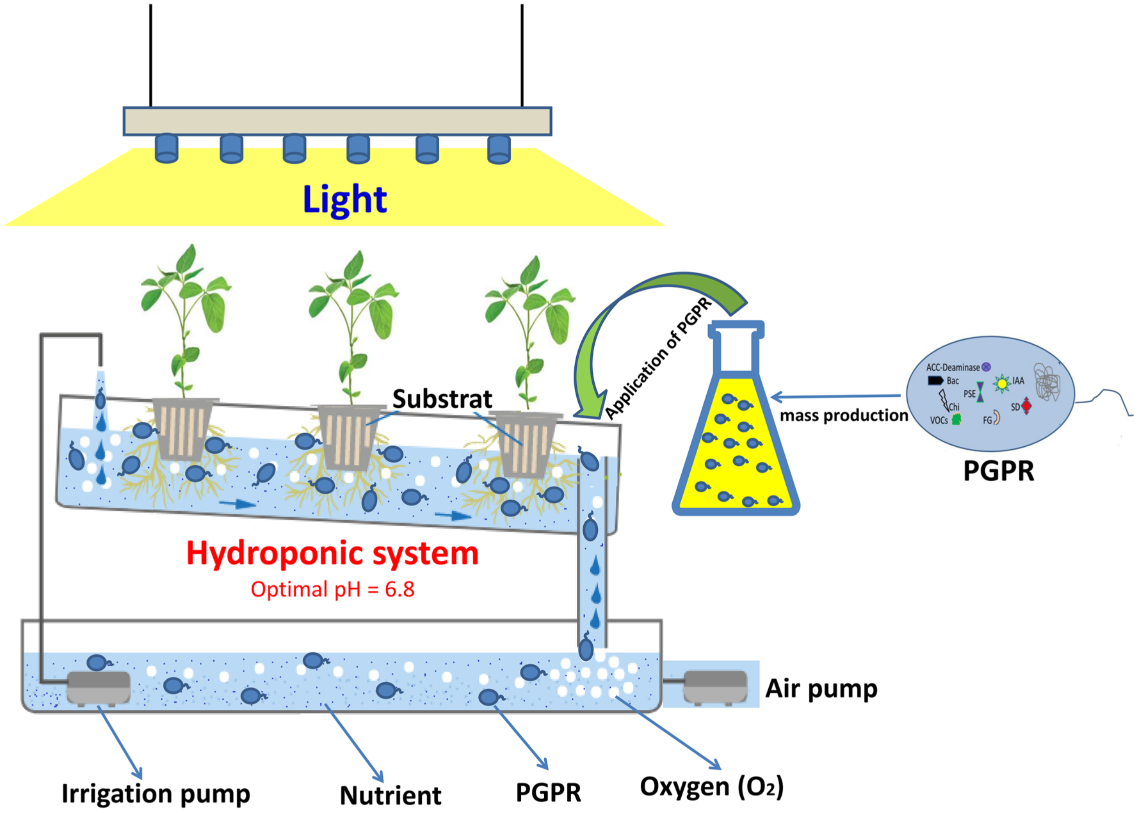

Fig. 2 Application of PGPR into the hydroponic system, modified from Hydroponic Urban Gardening Blog

predicted to increase. Additionally, the adoption of these technologies by farmers is expected to contribute to improving their quality of life and reducing the labor force (Akkoyunlu 2013).

The use of technological applications in agriculture has allowed the practical creation of controlled cultivation environments in controlled-environment agriculture (CEA). Many factors, such as light, humidity, soil, ventilation, irrigation, and fertilization, can be controlled with automation in greenhouses where CEA is performed, which provides the maximum benefit to plants (Sabir and Singh 2013; Othman et al. 2019). Greenhouses are structures built with the aim to optimize agricultural production per unit area, and this benefit can be maximized with soilless agricultural systems.

Soilless agriculture is a type of new-generation growing system that is based on providing a requisite amount of water and nutrients for plant life (Talaz and Nas 2019). In soilless agriculture, hydroponics involves the direct provision of nutrient solutions in a liquid environment, whereas solid culture (aggregate substrate) involves the growth of plant roots in peat, perlite, vermiculite, coco peat, rockwool, sand, sawdust, or pumice enriched with nutrient solutions.

The hydroponics system provides the opportunity to produce throughout the year without being dependent on the soil. It has been determined that the substrate used in soilless agriculture affects plant growth, fruit quality, and yield (Asaduzzaman et al. 2015; El-Kazzaz and El-Kazzaz 2017; Othman et al. 2019; Raviv et al. 2019; Kumar and Saini 2020; Lakhiar et al. 2020). Nihad et al. (2018) investigated yield and quality parameters in strawberries using five different substrates (volcanic tuff, coco peat + perlite, peat moss + perlite, tuff + cocopeat, and tuff + peat moss) and concluded that the coco peat, used as a potentially eco-friendly substrate in soilless strawberry culture, had a more positive effect on leaf physiology, fruit yield, and quality than the tuff. It has also been highlighted that berry fruits (grapes, raspberries, blackberries, blueberries, and strawberries) can be cultivated in soilless culture. This is especially true for strawberries and blueberries, which need environments where the nutrient contents can be controlled, and hydroponic systems are thus suitable for their cultivation (Kumar and Saini 2020). Moreover, another study showed that the addition of shredded corn stalk to a growing medium containing perlite and pumice can increase the fruit quality and yield of tomato (Tzortzakis and Economakis 2008). However, tomato plants cultivated in coconut substrate (cocopeat) showed higher vegetative growth than those cultivated in perlite medium (Jerca et al. 2015). Kılıc et al. (2018) reported that a medium containing coconut shells was the most suitable in terms of fruit quality of tomato, while perlite was more advantageous in terms of productivity.

Hydroponic systems involve the direct delivery of the nutrient solution to the plant root zone, and thus water and fertilizer can be used more efficiently than in other systems (Prakash et al. 2020). Crops grown in hydroponic systems had 20–25% higher yields than those grown under conventional agriculture. Furthermore, due to the controlled environmental conditions, the impact of climatic changes can be balanced with the help of these systems, resulting in a lack of negative effects on annual crop production (Markets and markets 2020). Additionally, problems caused by abiotic stress can be more easily overcome due to the abundant oxygen available in the system (Savvas et al. 2013; Raviv et al. 2019; Lakhiar et al. 2020). Although it has many advantages, such as the elimination of pesticides, reduced exposure to stress factors and high productivity, hydroponic systems have some disadvantages, such as high expenses, a lack of information and a shortage of qualified personnel (Macwan et al. 2020; Gonnella and Renna 2021).

Consequently, scientists should engage in training programs to provide more information about the potential of soilless agriculture for farmers. Despite some disadvantages, advances in soilless agriculture will likely continue in the future because of environmental pollution, growing populations and decreases in soil fertility.

The success of soilless agriculture

Soil is not an essential factor for the growth and development of plants. However, it provides all the macro- and micronutrients necessary for plant life. Traditional agriculture has certain disadvantages, such as the waste of irrigation water, the requirement of a large land area, and the use of large amounts of chemical fertilizers. Thus, soilless agriculture has garnered attention because of its elimination of these disadvantages. Thanks to the presence of a closed-loop system, soilless agriculture involves a fixed recycled water supply, retains 85–90% of the applied irrigation water, and provides better efficiency than traditional production (Pradhan and Deo 2019). Europe has been at the forefront of the application of advanced techniques in soilless horticulture, and countries, such as France, Spain, and the Netherlands, have large areas over which greenhouse cultivation is implemented. Furthermore, advances in smart technologies have supported the development of soilless agriculture in Europe. National government statistics indicate that the adoption of soilless agriculture (hydroponics) has been the highest in European countries. Hence, the market is highly improved in this region (Markets and markets 2020).

Nutrients, pH, oxygen, carbon dioxide, light and temperature can be easily adjusted and controlled in soilless agriculture, thus positively affecting the yield of plants, and deleterious elements present above certain dosages could be limited within safe dosages. In soilless agriculture, the surrounding environmental and root temperature and supply to roots can be controlled by oxygen. It is well known that water resources are decreasing worldwide. People should thus be very careful when using water, and soilless agriculture is important in protecting our water resources. Vegetables produced with soilless agriculture can be of high quality and need little washing. In soilless agriculture, irrigation water is accurately controlled in extremely lower amounts than in traditional agriculture (El-Kazzaz and El-Kazzaz 2017). In addition to the routine use of soilless agriculture in crop production, it is used in basic abiotic stress-based and plant genetic studies. In addition, it plays an important role in the development of new plant varieties suitable for the ever-changing climate characteristics resulting from global climate change.

The agricultural and physiological effects of salt stress on tomato, which is one of the most significant horticultural crops in the world, have been studied using different soilless agriculture practices (deep flow technique, nutrient film technique, and perlite substrate). These studies have shown that efficiency decreases in the following order: “deep flow technique > perlite > nutrient film technique” (Rodríguez-Ortega et al. 2019).

Chemutai et al. (2019) investigated the effects of nitrogen, phosphorus, and potassium (NPK) and plant tea (*Tithonia diversifolia*) manure with selected soilless growth media (100% natural soil, 100% sawdust, 100% charcoal dust, 100% coffee husks, sawdust + charcoal dust (1:1), sawdust + coffee husks (1:1), charcoal dust + coffee husks (4:1), and charcoal dust + saw dust + coffee husks (2:2:1)) on *Amaranthus cruentus* to identify alternative growth media for its production. Based on the results, the mixture of charcoal dust and dry coffee husks (4:1) along with the application of either NPK or plant tea manure was identified as the best alternative growth media. Another study using six different substrates [T1: coarse tuff + fine tuff + coco peat (5:1:4), T2: coarse tuff + medium tuff + fine tuff + coco peat (5:5:2:8), T3: medium tuff + fine tuff + coco peat (5:1:4), T4: medium tuff + fine tuff + peat moss (5:1:4), T5: perlite + medium tuff + fine tuff + coco peat (5:5:2:8), and T6: lightweight expandable clay aggregates (LECAs) + fine tuff + coco peat (5:1:4)] analyzed the growth, flower quality, and some morphological-physiological characteristics of violet (*Viola* × *wittrockiana*), Madagascar periwinkle (*Catharanthus roseus*), and Pavia lily (*Longiflorum* × Asiatic lily (*Lilium*) ‘Pavia’) and determined the most suitable substrate content for use in soilless agriculture. The LECA + coco peat mixture was reported to have the lightest weight in terms of field capacity, sufficient ventilation, and the best water-holding capacity. Moreover, it has been determined that LECA + organic matter substrate is the best mixture candidate in terms of physical properties (A'saf et al. 2020).

PGPRs as biofertilizers and biostimulators

An emerging method in agriculture is the use of soilless culture, which refers to any method of growing plants without soil as a rooting medium. This technique provides significant advantages over traditional methods by decoupling plant growth from soil-associated problems, such as soil-borne pests and diseases, decreased arability, salinity, and low soil quality (Tzortzakis et al. 2020). A plant biostimulator is defined by current European Union (EU) legislation on fertilizers as "any substance or microorganism, in the form in which it is supplied to the user, applied to plants, seeds or the root environment with the intention to stimulate natural processes of plants benefiting nutrient use efficiency and/or tolerance to abiotic stress, regardless of its nutrient content, or any combination of such substances and/or microorganisms intended for this use" (Traon et al. 2014). To this end, we focus on microbial plant growth-promoting (PGP) inoculants, which have been studied extensively in recent decades. These PGPR-based biostimulants are the main components of the biofertilizers used in agriculture (Calvo et al. 2014; Le Mire et al. 2016).

PGPRs release extracellular enzymes for the degradation of the cell wall of fungi that can also result in the suppression of phytopathogenic fungi. They can be excellent candidates for providing long-term induced resistance in plants (Egamberdieva et al. 2011; Joshi et al. 2012; Mbarki et al. 2017). Furthermore, heavy metal-resistant PGPRs have been identified that have proven their potential to promote plant growth under heavy metal stress possessing (Pramanik et al. 2018). The resistance mechanisms include some processes, such as intracellular bioaccumulation/biosorption, extracellular complexation with polysaccharides/siderophores and enzymatic metal transformation (Ahmad et al. 2016; Chen et al. 2016; Pramanik et al. 2016; Ayangbenro and Babalola 2017; Liu et al. 2018; Pramanik et al. 2018; Treesubsuntorn et al. 2018). These bacteria can assist heavy metal hyperaccumulator plants by accelerating their uptake, on the other hand, reduce the heavy metal uptake in non-hyper-accumulator and can minimize heavy metal accumulation in edible parts of the plants (Pramanik et al. 2018).

Recently, Awan et al. (2020) reported that two wheat (*Triticum aestivum* L.) varieties under heavy metal stress accumulated more heavy metal in the roots and shoots, resulting in severe oxidative stress, evident by an increase in malondialdehyde content. Additionally, they also observed that these varieties under stress altered antioxidant enzymes, such as catalase, ascorbate peroxidase and superoxide dismutase. However, the inoculation of two wheat varieties with *Bacillus siamensis* enhanced plant growth, reduced oxidative stress, and improved the activities of antioxidant enzymes in both varieties. As a result, *B. siamensis* reduced the metal toxicity in wheat varieties through the augmentation of the antioxidant defense system. Similarly, Ullah et al. (2019) found that endophytic *Serratia* sp.UI01 and *Enterobacter aerogenes* UI02 strains isolated from *Solanum nigrum* improved plant growth and reduced oxidative stress in *Brassica juncea* exposed to heavy metal (Cd) stress. They also observed that antioxidant enzymes and metabolites against reactive oxygen species including peroxidase, catalase, alcohol dehydrogenase, polyphenol oxidase, superoxide dismutase, reduced glutathione, malondialdehyde and flavonoid were significantly relieved by inoculation of IU01 and IU02 strains in the plant.

The key characteristics required for microbes to be considered PGPRs include the production of phytohormones, such as cytokinins, auxins, gibberellins, ethylene, and abscisic acid (Goswami et al. 2016; Saleem et al. 2017). These phytohormones facilitate plant cell enlargement and division and the extension of roots and influence the hormonal balance of plants. In addition to the production of phytohormones, free nitrogen fixation, phosphate solubilization, and SD production are important characteristics of PGPRs (Jha and Saraf 2015). Nitrogen serves as a critical component in the synthesis of proteins, cellular enzymes, RNA, DNA, and chlorophyll, which in turn enable plant growth (Oberson et al. 2013; Glick 2014). Additionally, phosphorus is the second-most crucial element after nitrogen, but its uptake by plants is limited because it exists in an insoluble form; rhizospheric bacteria are able to solubilize phosphate, thereby making it available for plant uptake (Vessey 2003). Similarly, bacteria present in the rhizosphere also release organic compounds for the chelation of Fe^{3+} (Payne 1994).

The use of PGPRs in soilless agriculture has been studied and examined by various research groups using different crops. Van Peer et al. (1991) grew cucumber, lettuce, and tomato plants hydroponically and used *Pseudomonas* sp. strain WCS417r as the PGP bacteria. This strain was not only used as a biostimulator but also served as a biocontrol agent against *Fusarium* through the increased production of phytoalexin. Another group used lettuce, tomato, and soybean plants, to which *B. subtilis* was applied for plant growth, and this PGP species affected the shoot growth of the plants under salt stress conditions (Yasufumi and Kaneaki 2003; Woitke et al. 2004; Balanza et al. 2012; Yasmin et al. 2020). Bisht et al. (2019) studied the alleviation of nutrient deficiency-induced stress in chickpea through the use of *Paenibacillus lentimorbus*, and a study conducted by Kuzmicheva et al. (2017) analyzed the soybean varieties Nice-Mecha, Bara, and Svapa in the presence and absence of *Pseudomonas oryzihabitans*.

Advances in the biotechnological applications of PGPRs

Soilless agriculture was initially developed to manage soil-borne plant diseases (Vallance et al. 2011). However, root rot epidemics have become a continual threat to crop production in commercial greenhouses that use soilless cultivation systems. Airborne dust, irrigation water, farm tools, and transplants are some of the main sources of pathogen contamination in such systems (Sutton et al. 2006). The use of PGPRs to suppress plant diseases is a newly emerging and valuable option in soilless cropping systems (Vallance et al. 2011; Sambo et al. 2019). Nevertheless, the rapid identification and utilization of these potential bacteria with classical microbiology methods is challenging (Franco-Duarte et al. 2019), as many PGPRs are overlooked because many relevant genes are not expressed in the absence of natural chemical triggers (Paterson et al. 2017).

The advancement of next-generation sequencing (NGS) methods has enabled researchers to further investigate and understand microorganisms around the globe from different perspectives (Cao et al. 2017). Genome mining, which involves the analysis of the whole-genome sequence data of a PGPR to identify the genes encoding beneficial bacterial enzymes and metabolites, has revolutionized the identification and use of potential beneficial microbes (Van Der Voort et al. 2015; Paterson et al. 2017). Several studies (Arruda et al. 2019; Eida et al. 2020; Zhou et al. 2020) have adopted a genome mining strategy to identify PGPR strains with novel antimicrobial gene clusters that have immense biocontrol potential and plant growth stimulatory effects. Furthermore, the reliable differentiation of potentially human pathogenic PGPR strains from nonpathogenic strains has been a challenge in bacterial diagnostics (Cosentino et al. 2013). However, genome sequencing coupled with machine learning approaches, such as PaPrBaG (Pathogenicity Prediction for Bacterial Genomes) (Deneke et al. 2017) and DeePaC (Deep Learning Approach to Pathogenicity Classification) (Bartoszewicz et al. 2020), has been reported to reliably discriminate potentially pathogenic strains from nonpathogenic strains.

The modern advances in sequencing technology have not only enabled more accurate classification of bacteria according to their genomes but also allowed for deeper taxonomic identification of complex microbiomes, which represent the combined genetic material of all microorganisms occupying an environment (Cao et al. 2017). Such advanced techniques have also enabled us to track the spatiotemporal dynamics of PGPRs using strain-specific primers designed from whole-genome sequence data (Zhang et al. 2018). Few studies (Mosimann et al. 2017; Mendis et al. 2018) have reported on qPCR-based methods successfully used to monitor the population dynamics of inoculants in nonsterile soil and plant roots, wherein complex microbial communities reside, let alone under soilless conditions. Furthermore, Jo et al. (2020) simultaneously monitored the population of a bioinoculant and the surrounding microbiota over time.

Advanced molecular biology tools have been used to describe the structure and diversity of the entire microbial community in various environments and can help to investigate the functional roles of such communities. Korenblum et al. (2020) stated that the microbial communities associated with roots provide specific functions to their hosts to help regulate plant growth, health, and productivity. Dong et al. (2019) also reported on the positive impact of natural microflora in controlling diseases of tomato seedlings in a soilless cultivation system. They found that *Pseudomonas*, which had been reported to improve plant growth and induce stress resistance in tomato and red pepper plants, was one of the most predominant genera in the nutrient solution. Furthermore, some beneficial PGP fungi, such as *Trichoderma virens* and *Trichoderma harzianum,* were detected. Sheridan et al. (2017) analyzed PGP microorganisms in the plant root zone microbiome in hydroponic cultivation systems for different crops through the use of amplicon sequencing targeting 16S rRNA genes. In their study, four different crops (durum wheat, bread wheat, potato, and soybean) were inoculated with a number of strains, including *Pseudomonas* spp., *Bacillus* spp., *Enterobacte*r spp., *Streptomyces* spp., *Gliocladium* spp., and *Trichoderma* spp. The authors concluded that the application of PGPRs to the plant root zone could change the microbial community even when only a small portion of the inoculated microbes colonized the root zone. Mamphogoro et al. (2020) used a similar technique to analyze the microbial communities associated with the sweet pepper *Capsicum annum* to identify potential biocontrol agents against pathogens. They found that the majority of the genera present in the communities consisted of *Acinetobacter*, *Agrobacterium*, and *Burkholderia*, which are known fungal antagonists. Similarly, Ye et al. (2020) found that *Corallococcus* sp. strain EGB controlled cucumber *Fusarium* wilt in a hydroponic system by migrating to the plant root and regulating the microbial community. In a different study, Hultberg et al. (2017) investigated the influence of the root microbiome in the presence of inoculated *Pythium ultimum* at three different stages of tomato plant growth; they reported that *P. ultimum* changed the composition of the microbial communities in the plant rhizoplane, wherein Bacteroidetes was the dominant phylum in the presence of *P. ultimum,* and Proteobacteria was more abundant in the control.

Another advancement in the biotechnological application of PGPRs is the use of transcriptomics. Understanding a transcriptome is essential for inferring the functional features of a genome and obtaining information on the molecular makeup of cells and tissues (Wang et al. 2009). Lee et al. (2016) made use of such an approach to gain insight into the responses of lettuce following treatment with the beneficial microbe *Pseudomonas chlororaphis*. This treatment led to the increased expression of genes involved in the response to pathogens and external stress. Moreover, the authors showed that the nodulin family, which is known to regulate phosphorylation and signaling and stimulate transport activity and resistance to osmotic and environmental stress, was expressed. Bharti et al. (2016) used a similar approach to identify the stress-responsive genes of wheat through inoculation with the PGP *Dietzia natronolimnaea* STR1. Their study confirmed the involvement of the ABA signaling cascade, as *TaABARE* and *TaOPR1* were upregulated in PGPR-inoculated plants, which led to the induction of *TaMYB* and *TaWRKY* expression followed by the stimulation of the expression of a plethora of stress-related genes. Their results also showed enhanced expression of *TaST*, a salt stress-induced gene associated with the promotion of salinity tolerance in PGPR-inoculated plants. A group led by Gómez-Godínez (2019) used metatranscriptomics to study nitrogen fixation in maize plantlets inoculated with a group of PGPRs (*R. phaseoli* Ch24-10, *A. brasilense* Sp7, *M. extorquens* AM1, *B. amyloliquefaciens* CCGE2031, *S. americanum* CFNEI 156, and *R. phaseoli* Ch24-10), which showed the expression of *Azospirillum nif* genes in the presence of the PGPRs. Another work by Yi et al. (2017) involved comparative transcriptomics of *Bacillus mycoides* strains in potatoes and provided insights into the transcriptomic profiles and survival strategies of plant-associated endophytes and soil isolates of this species.

Despite the plethora of studies performed to date, there remains a huge knowledge gap that needs to be addressed to commercialize PGPRs for sustainable soilless agriculture. Hence, the development of proper strategies and additional research and trials are required.

Future of PGPRs in soilless agriculture

In agricultural production systems, amending the soil with chemical fertilizers is considered indispensable for achieving optimum yield. However, it is well known that the constant and excessive use of chemical fertilizers disrupts the ecology of soil, affects the microbial population in the rhizosphere, pollutes groundwater and has harmful effects on human health (Ayala and Rao 2002; Joshi et al. 2006; Azizoglu et al. 2020). Therefore, the application of PGPRs in agricultural production has become popular because it significantly reduces the use of chemical fertilizers and pesticides. The use of PGPRs instead of harmful chemicals in modern agriculture is considered to be an excellent eco-friendly biotechnological approach (Pandey et al. 2012). PGPR application increases the germination rate, development of roots, yield, leaf area, chlorophyll ratio, nitrogen ratio, protein ratio, hydraulic activity, thirst tolerance, and root and stem weight, delays the aging of leaves and provides resistance to some diseases. In the field, PGPRs may not provide expected results due to unexpected conditions. Unfavorable environmental conditions, such as pH changes in the soil, high temperatures, low rainfall and humidity, and nutrient deficiencies, result in reduced microorganism colonization (Çakmakçı 2005). Because conditions are more controlled in soilless agriculture practices, successful microorganism colonization increases.

The presence of PGPRs increases plant resistance to stress, and they can be easily applied at any stage of the plant life cycle. Soilless agricultural practices and the application of PGPRs are likely to positively increase plant resistance to abiotic and biotic stress. PGPR application has positive effects on plant physiology and morphology to eliminate the harmful effects of stress, such as affecting plant water content, abnormal changes in hormone concentrations, and osmolytes (Yasmin et al. 2019).

Soilless agriculture is expected to become even more successful in combination with effective PGPR application. To date, some studies have provided clues to its success. PGPRs have been shown to increase lentil (*Lens culinaris*) growth and development under field and controlled environmental conditions (Zafar et al. 2012). Studies analyzing the effects of PGPR application on tomatoes (Kıdoğlu et al. 2009; Gul et al. 2012) and cucumbers (Gül et al. 2013) grown in a soilless agriculture system under greenhouse conditions have shown that PGPR application contributed positively to yield in both species (Table 1).

Baset Mia et al. (2010) examined the effects of PGPR application (*Bacillus sphaericus* UPMB10 and *Azospirillum* spp. Sp7 strains) on banana plantlets produced in nitrogen-free hydroponic culture. They reported that the Sp7 and UPMB10 strains increased banana seedling growth compared with that under control conditions and could be used as biofertilizers. Another study confirmed that *Azospirillum* spp. and *Azotobacter* spp. enhance the growth of strawberry (*Fragaria vesca*) in hydroponic culture (Rueda et al. 2016). Furthermore, it was reported that *Paenibacillus polymyxa* (SQR-21) increases watermelon growth in hydroponic culture (Yaoyao et al. 2017). In contrast with soil culture, aquaculture practices offer the ability to control and reuse beneficial microorganisms and manage nutrient availability. In fact, the naturally occurring microbial consortia of the hydroponics are a result of the presence of roots, and dormant endophytic microbes living in the seed can initiate growth simultaneously with the plant. Therefore, all hydroponic systems have a microflora in the rhizosphere under normal conditions. However, largely because it is dependent on the chemical compounds released from the plant roots, there might be differences between the systems due to physicochemical differences in the water content and the

Table 1 Some PGPRs successfully applied in soilless agriculture

Plant growth promoting rhizobacteria	Soilless cultures	Crops	References
B. amyloliquefaciens, B. brevis, B.circulans, B. coagulans, B. firmus, B. halodenitrificans, B. laterosporus, B. licheniformis, B. megaterium, B. mycoides, B. pasteurii, B. subtilis and P. polymyxa	Commercial substrate (SER CA-V7 Special semine, Vigorplant Italia Srl, Fombio, Italy), composed of a mixture of slightly or fully decomposed raised bog peat	Basil	Moncada et al. (2021)
P. polymyxa	Hydroponic	Watermelon	Yaoyao et al. (2017)
Azospirillum spp. and *Azotobacter* spp.	Hydroponic	Strawberry	Rueda et al. (2016)
P. putida, S. marcescens, Bacillus spp., *P. fluorescens, B. amyloliquefaciens*	Perlite	Cucumber	Gül et al. (2013)
B. subtilis, *A. vinelandi* and *C. pasteurianum*	Perlite cocopeat mixture in 1:1	Squash	Dasgan et al. (2012)
P. fluorescens bv3, *P. fluorescens* bv5 and *P. putida*	Perlite	Tomato	Gul et al. (2012)
PGPR, LCA strains. There is no identification of species	İn vitro, hydroponic and greenhouse (pot experiment)	Lentil	Zafar et al. (2012)
B. sphaericus and *Azospirillum* sp.,	Hydroponic	Banana	Baset Mia et al. (2010)
P. putida, *S. marcescens*, *P. fluorescens*, *B. amyloliquefaciens* and *Bacillus* spp.,	Perlite	Tomato	Kıdoğlu et al. (2009)
B. amyloliquefaciens	Perlite	Tomato	Gül et al. (2008)
P. fluorescens	Peat-based growing media	Tomato	Gagné et al. (1993)
P. putida	Hydroponic	Bean	Anderson and Guerra (1985)

environment surrounding the roots. For instance, hydroponic suspend roots in nutrient solution, and therefore, the compounds released from them are subject to relatively large dilution effects. On the other hand, solid cultures equipped with drip emitters are less disruptive as they do not create the same constant mass flow. The rhizosphere effect reaches further in hydroponics, yet the concentration of root exudates decreases much faster than in solid culture (Raviv et al. 2019; Söderström 2020).

While many publications focus on the PGPRs involved in the nitrogen cycle, others highlight the potential effects of PGPRs against plant pathogens in soilless culture (aquaponic systems) (Rakocy 2012; Gravel et al. 2015; Sirakov et al. 2016; Stouvenakers et al. 2019). Indeed, limited attention has been paid to the possible natural plant protection capacity of aquaponic microbiota. However, the potential of this protective action can be envisaged with regard to different elements already known to be involved in hydroponics or re-circulated aquaculture (Stouvenakers et al. 2019).

The suppression capacity demonstrated by the soilless medium is discussed by Postma et al. (2008) and Vallance et al. (2011). While some authors have comprehensively described plant pathogens, such as *Phytophthora cryptogea*, *Pythium* spp., *P. aphanidermatum* and *Fusarium oxysporum*, which are suppressed by the natural microbiota, they have not clearly identified the microorganisms responsible for this suppressive action (Stouvenakers et al. 2019). Suppressiveness in hydroponics can be interpreted as the pathogens not persisting or establishing, which also leads to little or no damage. The suppressive action of an environment can be related to the abiotic milieu. On the other hand, in most situations, suppressiveness is considered to be related directly or indirectly to microorganism activity or metabolites (Borneman and Becker 2007; Stouvenakers et al. 2019). Microbial inclusion in the suppressive effect in soilless agriculture is generally verified via the initial destruction of the microbiota of the soilless substrate by sterilization. Then, the beneficial microorganisms are reinoculated. In contrast to that in traditional culture, in which water recirculation does not occur, the suppressive activity in soilless culture can be explained by water recirculation, which allows for the enhanced development and dispersal of beneficial microorganisms (PGPRs) (Postma et al. 2008; Vallance et al. 2011; Stouvenakers et al. 2019). As a result, the combination of PGPRs and soilless agriculture is considered to be necessary for success in sustainable agriculture.

Conclusion and predictions

The use of PGPRs as a microbial fertilizer can be an excellent and environmentally friendly alternative to the application of chemical fertilizers. The success of PGPRs in the soil may decrease under adverse environmental conditions, such as high temperatures and soil pH, low precipitation and humidity, and nutrient deficiency, which reduce microorganism colonization in the rhizosphere. In soilless agriculture, however, these conditions are controlled, thereby putatively increasing successful PGPR colonization in such systems.

Because soilless agriculture utilizes recycled water, thanks to the use of a closed-circuit system, 85–90% of the irrigation water is maintained and it provides greater efficiency than traditional agriculture. Such systems can support beneficial microorganisms (PGPRs) by managing the water content (e.g., nutrient content, *C*/*N* ratio, oxygen and carbon dioxide concentrations) and parameters (e.g., temperature and pH). Moreover, water recirculation allows for the enhanced development and spread of PGPRs. For instance, when introducing a new microorganism normally not present into an aquaponics system, which is the combination of aquaculture and plants grown without soil, the selection of a microorganism adapted and safe for soilless culture is necessary.

Understanding how to include PGPRs in soilless agriculture to promote plant growth could enable the production of healthy and freshly grown crops and decrease the use of chemical fertilizers. Although some studies suggest that PGPRs can be successfully used in soilless agriculture, limited attention has been paid to their potential interactions. Indeed, the application of PGPRs in soilless agriculture is a promising technique. However, a better understanding of the role of bioinoculants in the uptake of nutrients needs to be established. Prior to the use of a particular bacterial strain, the proper assessment of the survival of the native bacteria within the plant of interest is needed to avoid negative impacts on plant growth.

In the future, it seems critical to investigate this interaction followed by the identification of the responsible beneficial microbes. Therefore, we strongly recommend the implementation of further research efforts on the interaction between soilless agriculture and PGPRs.

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