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EDITED BY

Nikolay Vassilev,
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Spain

REVIEWED BY

Joginder Singh,
Lovely Professional University,
India
Stefany Castaldi,
University of Naples Federico II, Italy

*CORRESPONDENCE

Khaled A. El-Tarabily
ktarabily@uaeu.ac.ae
Synan F. AbuQamar
sabuqamar@uaeu.ac.ae

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Plant growth-promoting microorganisms as biocontrol agents of plant diseases: Mechanisms, challenges and future perspectives

Mohamed T. El-Saadony¹, Ahmed M. Saad²,
Soliman M. Soliman³, Heba M. Salem⁴, Alshaymaa I. Ahmed⁵,
Mohsin Mahmood⁶, Amira M. El-Tahan⁷, Alia A. M. Ebrahim⁸,
Taia A. Abd El-Mageed⁹, Shaimaa H. Negm¹⁰, Samy Selim¹¹,
Ahmad O. Babalghith¹², Ahmed S. Elrys¹³,
Khaled A. El-Tarabily^{14,15,16*} and Synan F. AbuQamar^{14*}

¹Department of Agricultural Microbiology, Faculty of Agriculture, Zagazig University, Zagazig, Egypt,

²Department of Biochemistry, Faculty of Agriculture, Zagazig University, Zagazig, Egypt,

³Department of Internal Medicine and Infectious Diseases, Faculty of Veterinary Medicine, Cairo

University, Giza, Egypt, ⁴Department of Poultry Diseases, Faculty of Veterinary Medicine, Cairo

University, Giza, Egypt, ⁵Department of Agricultural Microbiology, Faculty of Agriculture, Beni-Suef

University, Beni-Suef, Egypt, ⁶Key Laboratory of Agro-Forestry Environmental Processes and

Ecological Regulation of Hainan Province, Hainan University, Haikou, China, ⁷Plant Production

Department, Arid Lands Cultivation Research Institute, The City of Scientific Research and

Technological Applications, Alexandria, Egypt, ⁸Jiangsu Key Laboratory for Microbes and Genomics,

School of Life Sciences, Nanjing Normal University, Nanjing, China, ⁹Department of Soils and

Water, Faculty of Agriculture, Fayoum University, Fayoum, Egypt, ¹⁰Department of Home Economic,

Specific Education Faculty, Port Said University, Port Said, Egypt, ¹¹Department of Clinical

Laboratory Sciences, College of Applied Medical Sciences, Jouf University, Sakaka, Saudi Arabia,

¹²Medical Genetics Department, College of Medicine, Umm Al-Qura University, Makkah,

Saudi Arabia, ¹³Soil Science Department, Faculty of Agriculture, Zagazig University, Zagazig, Egypt,

¹⁴Department of Biology, College of Science, United Arab Emirates University, Al-Ain, United

Arab Emirates, ¹⁵Khalifa Center for Genetic Engineering and Biotechnology, United Arab Emirates

University, Al-Ain, United Arab Emirates, ¹⁶Harry Butler Institute, Murdoch University, Murdoch, WA,
Australia

Plant diseases and pests are risk factors that threaten global food security. Excessive chemical pesticide applications are commonly used to reduce the effects of plant diseases caused by bacterial and fungal pathogens. A major concern, as we strive toward more sustainable agriculture, is to increase crop yields for the increasing population. Microbial biological control agents (MBCAs) have proved their efficacy to be a green strategy to manage plant diseases, stimulate plant growth and performance, and increase yield. Besides their role in growth enhancement, plant growth-promoting rhizobacteria/fungi (PGPR/PGPF) could suppress plant diseases by producing inhibitory chemicals and inducing immune responses in plants against phytopathogens. As biofertilizers and biopesticides, PGPR and PGPF are considered as feasible, attractive economic approach for sustainable agriculture; thus, resulting in a “win-win” situation. Several PGPR and PGPF strains have been identified as effective BCAs under environmentally controlled conditions. In general, any MBCA must overcome certain challenges before it can be registered or widely utilized to control diseases/pests. Successful MBCAs offer a practical solution to improve greenhouse crop performance

with reduced fertilizer inputs and chemical pesticide applications. This current review aims to fill the gap in the current knowledge of plant growth-promoting microorganisms (PGPM), provide attention about the scientific basis for policy development, and recommend further research related to the applications of PGPM used for commercial purposes.

KEYWORDS

biofertilizers, biopesticide, crop yield, disease suppression, pathogen suppression, plant growth-promoting rhizobacteria

Introduction

Plant pathogens and pests can have a large impact on agricultural productivity. Plant diseases reduce yields by 21–30% in several important crops worldwide (Savary et al., 2019). Meanwhile, certain plant pathogens have developed long-term resistance against chemical management (Lucas, 2011). Some economically important plant diseases have become more prevalent. Dependence on chemical pesticides has become one of the most pressing challenges to global environmental sustainability and public health (Fones et al., 2020). Because many of insecticides are difficult to break down into simpler components that are less dangerous, toxic residues remain in the soil; thus, posing health concerns (Gilden et al., 2010). Awareness of the environmental and health risks associated with synthetic chemical pesticides is highly recommended for sustainable crop management and less used chemicals (Donley, 2019).

Synthetic agrochemicals have been considered unsustainable, causing the quest for more environmentally friendly alternatives. The focus of modern agriculture research has turned to farm practices. Plant growth-promoting rhizobacteria (PGPR) are effective, environmentally safe, and non-toxic naturally occurring microorganisms that can serve as a promising alternative to chemical pesticides. Besides, environmental factors can affect agricultural productivity; thus, this may worsen the scenario in a variety of ways. We have many reasons to take serious actions toward plant disease control management to improve our health and reduce the effects of environmental stresses (Chaloner et al., 2021). Biological control provides one of the most economical and long-term effective strategies for managing plant diseases and reducing crop loss.

Recent advances in our understanding of plant growth-promoting microorganisms (PGPMs) warrant a proper scientific evaluation of the relationship between the properties of PGPMs and their impact on plant growth, yield, and resistance/tolerance to biotic and abiotic stresses. In addition, this review study builds on a growing body of literature concerning some potential implementations of PGPMs in sustainable agriculture. Here, the aim is to provide a state-of-knowledge review reporting the effects of PGPMs on plants and finding solutions to the challenges that

face microbial biological control agents (MBCAs) when applied on a large scale compared with those of chemicals.

PGPR as promising biocontrol agents

Soil is a complex ecosystem containing various groups of microorganisms, including bacteria, fungi, protists, and animals (Müller et al., 2016). These microorganisms play key roles in plant development, nutrient regulation, and biocontrol activities. They settle in the rhizosphere and endo-rhizosphere of plants, where they use a variety of direct and indirect processes to support plant growth. Lyu et al. (2020) have stated that the phytomicrobiome (plant-associated microorganisms) can provide competitive, exploitative, or neutral alliances with plants; thus, affecting crop yield. Recently, scientists have looked deeply into employing beneficial PGPR to inhibit phytopathogens and promote plant growth (Qiao et al., 2017; Alwahshi et al., 2022). A key part of this might be attributed to the enhancement of target specificity between PGPR and the plant species (Lommen et al., 2019).

According to Zgadzaj et al. (2016), rhizosphere microbiome refers to bacterial, archaeal and fungal communities as well as their genetic material closely surrounding plant root systems. Microorganisms can indirectly impact crop health and phenotypic plasticity by influencing the growth of plants and defense responses due to their co-evolution with plants on a large scale (Goh et al., 2013). The rhizosphere is home to various microorganisms that provide steady PGPR supplies (Antoun and Kloepper, 2001). The phytomicrobiome includes the bacterial population that colonize the rhizosphere, on the root surface, and between the root cortex cells (Inui Kishi et al., 2017). Since plants can first colonize the terrestrial environments, PGPR have co-evolved with related plants; resulting in synergistic host plants' relationships (Gouda et al., 2018). The effects, methods, and possibility for successfully applying PGPR to agricultural plant production in controlled situations have been the subject of numerous studies. This is critical for developing more widely used methods of biological control that consider field settings.

Safety and quality control are more crucial in vegetable cultivation since we use them less processed or unprocessed, and they have impact on health. PGPR are more achievable under greenhouse conditions. Because of the controlled environment, a significant number of prospective BCA has been discovered, and maybe ready for placement (Singh et al., 2017); thus, they have been confirmed to be successful in greenhouse investigations (Liu et al., 2018). *Bacillus subtilis*, *Bacillus amyloliquefaciens* and *Pseudomonas stutzeri* are among those shown to achieve success in root colonization as well as prevention of the pathogen *Phytophthora capsici* in cucumber (Islam et al., 2016). At the post-harvest stage, *B. subtilis* can protect tomato fruits from infection by *Penicillium* sp. and *Rhizopus stolonifer* (Punja et al., 2016).

Under greenhouse conditions, *B. amyloliquefaciens* isolates, diminish *Fusarium oxysporum* causing *Fusarium* wilt disease (Gowtham et al., 2016). In controlled situations, PGPR -as BCAs- are effective, indicating their role in greenhouse production systems and their efficacy in commercial horticulture. It is not necessary to distinguish the indirect PGPR pathways for pathogen infection avoidance and plant growth promotion under abiotic stresses. In addition, PGPR with biocontrol activities that also enhance plant growth would be more effective in practice. Plant tolerance to abiotic conditions and resistance to phytopathogens causing plant diseases can be improved by PGPR (Bhat et al., 2020; Leontidou et al., 2020). Some strains benefit plants' coping with stress and flourishing in abiotic environments (Goswami and Deka, 2020).

While most researchers have reported PGPR under these controlled conditions, few of them have investigated their effectiveness as BCAs, especially when combined with an abiotic stress. This is a critical factor in field biocontrol, and when climate change affects the ecosystem. The long synergism between PGPR and plant may deliver various benefits to the host plant (Fan et al., 2020).

Biocontrol mechanisms using PGPR

PGPR can enhance the availability of certain nutrients [phosphate solubilization and nitrogen (N₂) fixation], or synthesize the phytohormones [indole-3 acetic acid (IAA), ethylene (ET), jasmonic acid (JA), gibberellic acid (GA), and cytokinins (CKs); Mengiste et al., 2010; Vejan et al., 2016; Gouda et al., 2018; Sham et al., 2019].

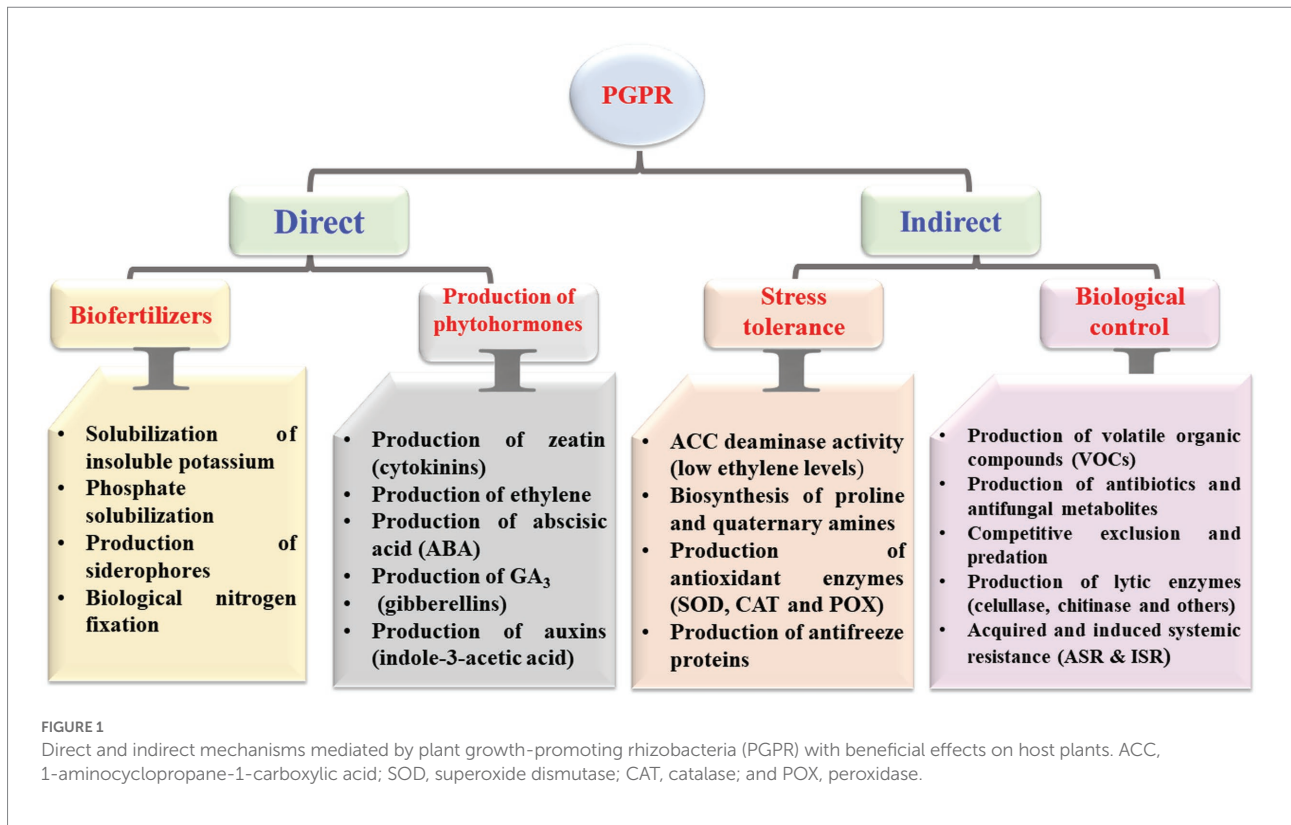
PGPR colonizing a host plant can stimulate its growth through direct and indirect mechanisms (Figure 1). Direct mechanisms include the production of plant hormones, solubilization of phosphates, and increased uptake of iron. Indirect effects include antibiotics production, nutritional competition, parasitism, pathogen toxin inhibition, and induced resistance (Elnahal et al., 2022). The attitude of "PGPR" in creating phytohormones, molecules of signaling metabolites, and related substances describe how plants protect themselves from drought as an

example of abiotic stress and salinity (Jochum et al., 2019). According to Abbas et al. (2019), PGPR may also alter the shape of the roots, resulting in increased root surface and improved root performance. In addition, PGPR can compete with other bacteria by colonizing rapidly and accumulating a greater supply of nutrients, preventing other organisms from growing (Salomon et al., 2017, Abd El-Mageed et al., 2020). PGPR have different strategies to colonize, of which each is tied to a particular host (Choudhary et al., 2011). In general, pathogen infections can be suppressed by using antibiotics and antifungal metabolites; thus considered a well-known direct biological control strategy (Raaijmakers et al., 2002). Bacteriocins, antibacterial proteins, and enzymes are examples of antimicrobial peptides (Compant et al., 2005). Antibiotics are small antimicrobial molecules produced by PGPR that can inhibit the process of metabolic or growth activities of microbial pathogens (Duffy et al., 2003). These antibiotics, which are mostly strain-specific, can target the ribosomal RNA (rRNA), alter the membrane structure, and damage the cell walls of bacterial pathogens (Abriouel et al., 2011; Maksimov et al., 2011; Nazari and Smith, 2020).

Many bacteria produce bacteriocins, where some have a greater variety of inhibitory activities than others (Abriouel et al., 2011). Siderophores are specialized chelating agents of ferric iron that inhibit phytopathogens from gaining access to iron; thus, maintaining plant health particularly in iron-deficient environments (Shen et al., 2013). PGPR can manage various plant diseases by depriving pathogens of iron, thereby reducing disease development and generating extracellular siderophores (Radzki et al., 2013). Bacteriocins, siderophores, and antibiotics have thus been identified as the three supreme operative approaches for potential biocontrol prior to *in vivo* applications (Kloepper et al., 1980). Several studies have investigated PGPR as a potential plant disease management tool to synthesize plant-beneficial metabolites such as siderophores (Subramanian and Smith, 2015).

PGPR can indirectly increase crop stress tolerance. Signal chemicals, such as phytohormones and specialized signal molecules, enable plant-to-microbe and microbe-to-plant communication (Lyu et al., 2020). The control and regulation of activities in the holobiont include the host plant and the "specific" phytomicrobiome (the plant-phytomicrobiome interaction). Two microbe-to-plant signals, lipochitooligosaccharides (LCOs) and thuricin17 (TH17), enhance stress tolerance in different plant species (Lyu et al., 2020). Resistance-inducing and antagonizing PGPR might be useful as new inoculants with combinations of different mechanisms of action, leading to a more efficient use for biocontrol strategies and plant growth promotion (Glick, 1995).

PGPR can also produce volatile organic compounds (VOCs) that play a significant role in plant growth and induced systemic resistance (ISR) to pathogens (Raza et al., 2016). Beneduzi et al. (2012) found that PGPR can trigger ISR as a strategy to improve disease resistance of plants. Roots colonization by arbuscular mycorrhizal fungi (AMF) and certain strains of non-pathogenic bacteria can improve plant resistance to biotic stresses



(Mauch-Mani et al., 2017; Pérez-de-Luque et al., 2017). ISR triggered by PGPR and plant growth-promoting fungi (PGPF) can be found in a wide range of plant taxa (Bhattacharyya and Jha, 2012). Systemic acquired resistance (SAR); however, can be activated by a pathogen infection (Gao et al., 2015). Salicylic acid (SA) signaling is associated with the production of pathogenesis-related (PR) genes. Unlike SAR, ISR functions independently of SA, but requires responses to ET and JA. This can be achieved by the induction of defense-related gene expression; although is not always associated with induced PR proteins (Mathys et al., 2012).

Previous studies have identified ISR to stimulate PGPR via the SA-dependent pathway rather than the JA/ET-dependent pathway (Takishita et al., 2018). Other plant hormones, such as auxins, GA, CKs and brassinosteroids, may also contribute to plant immunity (Nakashita et al., 2003; Kazan and Manners, 2009; Giron et al., 2013; Rady et al., 2021). Hormonal crosstalk is thought to allow the cultivation and exert their immunological growth and defense reactions (Pieterse et al., 2014; AbuQamar et al., 2017; Sham et al., 2017).

PGPR are involved in diverse mechanisms to enhance plant growth and/or act as BCAs. Crop production promotion and disease management could be investigated together to ensure sustainability and cost-effectiveness of agricultural systems. Thus, effective PGPR strains can promote stress tolerance and nutrient absorption, plant development, and battling fungal/bacterial diseases. Thus, this appears to be a win-win situation to the PGPR strain and the host plant.

Challenges of employing PGPR as BCAs

PGPR-based biocontrol provides effective and long-lasting disease management. Europe and the United States are the most promising marketplaces for biocontrol products, followed by South America (Barratt et al., 2018). Although many PGPR have been tested *in vitro* and commercially proven as BCAs, new biocontrol products have been released from research activities carried out in the United States and Europe (Glick, 2012; O'Brien, 2017; Rosier et al., 2018). In general, the market of BCAs and their products is growing; yet, it is not well-adopted compared with chemical pesticides as the most common crop management method (Mishra et al., 2015).

Before being publically accepted/registered as a commercial BCA, there are certain requirements/needs that have to be taken into consideration (Bashan et al., 2014). As such, researchers should improve the efficacy of BCAs to manage certain disease(s). This can be achieved by having a BCA that has as many beneficial characteristics and mechanisms of action as possible. Such characteristics may include, but not limited to, the ability of the BCA to grow fast *in vitro*, produce a wide range of bioactive metabolites, possess high rhizosphere competence abilities, enhance plant growth performance, be environmentally safe, have the compatibility with other rhizobacteria/fungi, and be tolerant to abiotic stresses (Lyu et al., 2020). Successful colonization of root tissues and/or the rhizosphere is a critical component for any

PGPR strain to be an effective BCA; thus, to perform well against plant pathogens. On the other hand, performance of the inoculated PGPR may vary, depending on the survival rate in the soil, crop compatibility, interaction with other local microbial species and the environmental factors (Vejan et al., 2016). Survival and colonization are major components when identifying effective BCA isolates. *In vitro* antagonism experiments are often used to investigate the effect of bacterial isolates on certain diseases, prior to greenhouse and/or field trials (Bashan et al., 2014).

Performance of PGPR is generally assessed according to the geographical areas, soil types, host crop species, and under various environmental conditions (Choudhary et al., 2011). BCA growth is often easier to monitor under controlled conditions, i.e., greenhouses. The preference of this stage by most researchers could be attributed to the stability of environmental conditions. Greenhouse experiments evaluating the performance of BCAs under controlled conditions can provide strong theoretical and practical support for the application of PGPR in the field. Thus, this ensures the feasibility and efficacy of PGPR for commercial horticulture production, disease management and climate change conditions such as those found under field conditions.

PGPR stability is also influenced by the method, formulations, transportation, and storage conditions. To achieve high levels of the BCA survival (McIntyre and Press, 1991), one should improve the formulation technology (Lobo et al., 2019), increase the shelf-life of the BCA product (Carrasco-Espinosa et al., 2015), optimize the production of targeted microbial types (Zhang et al., 2019) and achieve low-cost production at large scales (Kang et al., 2017). Many scientists have attempted to extend the shelf-life of PGPR by decreasing the storage temperature and/or modifying the combinations of additives (Lee et al., 2016; Berger et al., 2018). Extensive research on the risks and benefits of BCAs is also required, because agricultural disease management approaches rely on this balance.

Due to the diverse modes of action, identification, characterization, the registration of promising PGPR strains take time and require academic-industry collaborations. Using natural sources (e.g., BCAs) to control pathogens also poses a set of legal and ethical issues that may threaten the local biodiversity (Hajek et al., 2016). In that regard, new species/populations of BCAs have been restricted from entering specific countries. For commercial uses, the application of PGPR in protected environments such as greenhouses is much easier, due to a more isolated and controlled environment delivery and potentially less negative ecological consequences. Another challenge that is linked to the widespread implementation of PGPR-based biocontrol is the regulatory problems. Currently, each country has its regulatory system that greatly vary among them (Bashan et al., 2014).

High development costs for new commercial BCAs, for example, have been identified as a barrier to the BCA industry's expansion in Australia (Begum et al., 2017). The high regulatory expenses of importing new BCAs into Australia is one of the most serious challenges. BCA registration requires tight coordination among governmental institutes, universities, and industrial sectors

to facilitate the assessment and commercialization of new BCAs and their products. The shortage of programs for financial and ecological benefits can also be added as a challenging problem (Heimpel et al., 2013). For global marketing and local practical applications, commercialization should follow international legislation. The International Biological Control Organization (IOBC) have gathered academicians, researchers and practitioners from different sectors/fields to identify the barriers and provide recommendations to overcome these limitation (Barratt et al., 2018).

When compared to chemical pesticides, which are more reliable and predictable, farmers could notice little or no economic gain. Such programs, including local seminars, training workshops and free conferences may increase awareness about the application of BCA in specific farming areas. Finally, PGPR-based biocontrol can hold a lot of promises to reduce agrochemicals use in agriculture. The widespread use of PGPR as BCAs requires massive effort from regulatory bodies and crop growers to convince the public and earn their trust in the capacity of the new BCA products to manage diseases and increase crop yields. High-value crop production in greenhouses could be an ideal place to test the efficacy of PGPR as BCAs in response to different abiotic stresses. Based on recent successful greenhouse trials, BCAs can be used in the field for managing disease and associated agricultural plant growth enhancement (Alwahshi et al., 2022).

Rhizobacteria as BCAs

In the past few decades, rhizobacteria have gained attention when applied to grains, seeds, roots, and/or soils to help the plant grow and develop. Rhizobacteria are important for N₂ fixation, promotion of plant growth, and biological control of plant pathogenic microorganisms. Recently, various microbial species are presently used in bacterization, containing *Azospirillum*, *Azotobacter*, *Bacillus*, *Rhizobium*, *Serratia*, *Stenotrophomonas*, *Streptomyces*, *Acinetobacter*, *Agrobacterium*, *Alcaligenes*, *Arthrobacter*, *Bradyrhizobium*, *Frankia*, *Pantoea*, *Pseudomonas*, and *Thiobacillus* (Whipps, 2001). Many plant diseases associated with nematodial, bacterial and fungal infections have been reported to be managed by PGPR. The use of BCAs has been controversial in suppressing nematode populations because other soil microorganisms and the host plant can be adversely affected. To manage diseases associated with plant-parasitic nematodes a combination of biological management, nematicides, organic soil amendments, and crop rotation have been used (Timper, 2011). *In vitro* culture filtrates of a strain of *Pseudomonas* sp. can suppress juvenile mortality of *Meloidogyne javanica*; thus, considerably reduce root gall and nematode population, and enhance plant development and yield (Nasima et al., 2002). Furthermore, inoculations with *Bacillus* spp. affect nematode behavior and feeding (Viaene et al., 2006). *Pseudomonas striata*, *Pseudomonas fluorescens*, and *B. subtilis* strains also overturn the population of nematodes (Table 1; Khan et al., 2012). Root-knot nematode

TABLE 1 Bacterial and fungal plant growth-promoting strains used as biocontrol agents against plant pathogenic microorganisms.

| Host | Pathogen | Disease | PGP strains Bacteria/Fungi | References |
|-------------------------------|--|---------------------------------------|--|--|
| I. Bacteria | | | | |
| Soybean | <i>Fusarium solani</i> , <i>Macrophomina phaseolina</i> | Root rot | <i>Bradyrhizobium</i> sp. | Parveen et al., 2019 |
| | <i>Sclerotinia sclerotiorum</i> | White mold | <i>Butia archeri</i> | Vitorino et al., 2020 |
| Pigeon pea | <i>Fusarium udum</i> | <i>Fusarium</i> wilt | Rhizobacteria spp. | Dukarea and Paulb, 2021 |
| | <i>Erwinia tracheiphila</i> | | <i>Glutamicibacter</i> spp. FBE-19 | Fu et al., 2021 |
| Apple | <i>Mucor piriformis</i> | <i>Mucor</i> rot | <i>Pseudomonas fluorescens</i> | Wallace et al., 2018 |
| Rice | <i>Meloidogyne incognita</i> | Root-knot nematode | <i>Trichoderma citrinoviride</i> Snef1910 | Tariq et al., 2020 |
| | <i>Magnaporthe oryzae</i> | Blast disease | <i>Pseudomonas putida</i> BP25 | Ashajyothia et al., 2020 |
| | <i>Xanthomonas axonopodis</i> pv. <i>glycines</i> | Bacterial pustule | <i>Pseudomonas parafulva</i> JBCS1880 | Kakembo and Lee, 2019 |
| | <i>Phytophthora capsici</i> | NA | <i>Pseudomonas</i> , <i>Burkholderia</i> | Khatun et al., 2018 |
| | <i>Xanthomonas oryza</i> | Bacterial leaf blight | <i>Bacillus subtilis</i> strain GBO3 | Faizal Azizi and Lau, 2022 |
| Strawberry | <i>Macrophomina phaseolina</i> | Charcoal rot disease | <i>Azospirillum brasilense</i> | Viejobueno et al., 2021 |
| | <i>Botrytis cinerea</i> | Gray mold | <i>Bacillus amyloliquefaciens</i> Y1 | Maung et al., 2021 |
| Cotton | <i>Macrophomina phaseolina</i> | Charcoal rot disease | <i>Pseudomonas aeruginosa</i> and <i>Sargassum ilicifolium</i> | Rahman et al., 2017 |
| | <i>Colletotrichum gossypii</i> | Ramulosis disease | <i>Bacillus amyloliquefaciens</i> , and <i>Bacillus velezensis</i> | Ferro et al., 2020 |
| Citrus fruit | <i>Penicillium digitatum</i> | Blue mold | <i>Bacillus megaterium</i> | Mohammadi et al., 2017 |
| Oil seed rape | <i>Sclerotinia sclerotiorum</i> | <i>Sclerotinia</i> stem rot | <i>Trichoderma atroviride</i> | Hidayah et al., 2022 |
| <i>Brassica campestris</i> L. | | Sclerotinose | <i>Bacillus thuringiensis</i> | Wang et al., 2020 |
| Canola | | <i>Sclerotinia</i> stem rot | <i>Paenibacillus chlororaphis</i> | Savchuk and Fernando, 2004 |
| Maize | <i>Fusarium graminearum</i> | Stalk rot | <i>Bacillus methylotrophicus</i> | Cheng et al., 2019 |
| Wheat | <i>Stagonospora nodorum</i> | <i>Stagonospora nodorum</i> blotch | <i>Bacillus subtilis</i> 26DCryChS | Maksimov et al., 2020 |
| | <i>Rhizoctonia solani</i> AG-8 | Wheat root pathogen | <i>Bacillus subtilis</i> | Zhang et al., 2021a |
| Pepper | <i>Phytophthora capsici</i> | Blight and fruit rot | <i>Bacillus licheniformis</i> BL06 | Li et al., 2020 |
| Tomato | <i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i> | <i>Fusarium</i> wilt | <i>Brevibacillus brevis</i> | Liu et al., 2022 |
| | <i>Rhizoctonia solani</i> | Damping-off | <i>Burkholderia cepacia</i> BY | Al-Hussini et al., 2019 |
| Mango | <i>Lasiodiplodia theobromae</i> | Dieback | <i>Streptomyces samsunensis</i> UAE1, <i>Streptomyces cavourensis</i> UAE1, <i>Micromonospora tulbaghiae</i> UAE1 | Kamil et al., 2018 |
| Tea | <i>Colletotrichum</i> sp, | Shoot necrosis | <i>Trichoderma camelliae</i> | Chakruno et al., 2022 |
| Date palm | <i>Fusarium solani</i> | Sudden death syndrome | <i>Streptomyces polychromogenes</i> UAE2, <i>Streptomyces</i> <i>coeruleoprunus</i> UAE1 <i>Streptomyces tendae</i> UAE1, <i>Streptomyces violaceoruber</i> UAE1 | Alblooshi et al., 2022 |
| | <i>Thielaviopsis punctulata</i> | Black scorch | <i>Streptomyces globosus</i> UAE1 | Saeed et al., 2017 |
| Royal poinciana | <i>Neoscytalidium dimidiatum</i> | Stem canker | <i>Streptomyces rochei</i> UAE2, <i>Streptomyces coelicoflavus</i> UAE1 and <i>Streptomyces antibioticus</i> UAE1 <i>Streptomyces griseorubens</i> UAE2 | Al Raish et al., 2021 |
| Banana | <i>Fusarium</i> spp. | Postharvest diseases | <i>Trichoderma</i> spp. | Al Hamad et al., 2021 Snehalatharani et al., 2021 |
| II. Fungi | | | | |
| Rice | <i>Helminthosporium oryzae</i> , <i>Bipolaris oryzae</i> | Leaf brown spot | <i>Trichoderma viride</i> , <i>Trichoderma</i> <i>harzianum</i> , <i>Trichoderma</i> <i>hamatum</i> | Khalili et al., 2012; Mau et al., 2022 |

(Continued)

TABLE 1 (Continued)

| Host | Pathogen | Disease | PGP strains Bacteria/Fungi | References |
|----------------------|---|------------------------------|--|---|
| Scorzonera | <i>Alternaria scorzonerae</i> , <i>Fusarium culmorum</i> | Root and stem rot | <i>Trichoderma harzianum</i> T-22 <i>Trichoderma</i> spp. <i>Trichoderma aggressivum</i> | Patkowska, 2021 Bilesky-José et al., 2021 Sánchez-Montesinos et al., 2021 |
| | <i>Sclerotinia sclerotiorum</i> , <i>Botrytis cinerea</i> , <i>Fusarium solani</i> , <i>Fusarium cucurbitae</i> , <i>Pythium aphanidermatum</i> , <i>Rhizoctonia solani</i> , <i>Mycosphaerella melonis</i> | | | |
| Tobacco | <i>Fusarium</i> , <i>Rubrobacter</i> , and <i>Talaromyces</i> spp. | Root rot | <i>Paenibacillus polymyxa</i> <i>Trichoderma harzianum</i> | Yao et al., 2021 |
| Okra | <i>Meloidogyne incognita</i> | Root-knot disease | <i>Trichoderma virens</i> | Tariq et al., 2018 |
| Beans | <i>Botrytis cinerea</i> | Chocolate spot | <i>Trichoderma atroviride</i> | Yones and kayim, 2021 |
| | <i>Sclerotinia sclerotiorum</i> | Wild mold | <i>Trichoderma asperellum</i> | Zapata-Sarmiento et al., 2020 |
| Onion | <i>Sclerotium cepivorum</i> | White rot | | Rivera-Méndez et al., 2020 |
| Tomato | <i>Colletotrichum gloeosporiodes</i> | Crop loss | <i>Trichoderma longibranchiatum</i> | De la Cruz-Quiroz et al., 2018 |
| Cabbage | <i>Fusarium oxysporum</i> | Cabbage <i>Fusarium</i> wilt | <i>Rhizobactrin</i> | Khafagi et al., 2020 |
| | <i>Sclerotium sclerotiorum</i> | Cabbage wilt | <i>Trichoderma hamatum</i> | Jones et al., 2014 |
| Cocoa | <i>Phytophthora Palmivora</i> | Black pod | <i>Aspergillus fumigates</i> | Adebola and Amadi, 2010 |
| Tomato | <i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i> | Wilt | <i>Penicillium oxalicum</i> | Murugan et al., 2020 |
| | <i>Rhizophagus intraradices</i> | Verticillium wilt | <i>Penicillium pinophilum</i> | Ibiang et al., 2021 |
| | <i>Meloidogyne javanica</i> | Root-knot disease | <i>Paecilomyces lilacinus</i> | Hanawi, 2016 |
| <i>Vigna radiata</i> | <i>Meloidogyne incognita</i> | | <i>Purpureocillium lilacinum</i> | Khan et al., 2019 |
| Pineapple | <i>Meloidogyne javanica</i> | | <i>Purpureocillium lilacinum</i> | Kiriga et al., 2018 |
| Carrot | | | <i>Pochonia chlamydosporia</i> | Bontempo et al., 2017 |
| Kiwi | Postharvest diseases Soil-borne pathogens | Kiwi fruit wound | <i>Debaryomyces hansenii</i> Rhizosphere | Sui et al., 2021 Tsegaye et al., 2018 |
| Tomato | <i>Sclerotium rolfsii</i> | Southern blight | <i>Stenotrophomonas maltophilia</i> PPB3 | Sultana and Hossain, 2022 |
| | <i>Phytophthora infestans</i> | Late blight | <i>Rhizopus</i> spp. | Agbor et al., 2021 |
| Peaches | <i>Monilinia laxa</i> | Postharvest fruit decay | <i>Aureobasidium pullulans</i> | Di Francesco and Baraldi, 2021 |
| Sweet potato | <i>Ceratocystis fimbriata</i> | Black rot disease | <i>Pseudomonas chlororaphis</i> subsp. <i>aureofaciens</i> SPS-41 | Zhang et al., 2021b |
| Rice | <i>Pyricularia oryzae</i> | Rice blast fungus | Rhizobacteria | Nabila and Kasiamdari, 2021 |
| Chickpea | <i>Rhizoctonia bataticola</i> | Chickpea dry root rot | <i>Bacillus subtilis</i> | Chiranjeevi et al., 2021 |

(RKN) infestations have been successfully managed via biological management using *Bacillus* isolates (Lee and Kim, 2016). Few studies have reported the endophytic *P. fluorescens* and *Bacillus* spp. to promote systemic resistance in crops against nematodes owing to the increased activities of phenylalanine ammonia-lyase, polyphenol oxidase, and peroxidase, as defense-related enzymes for producing antagonistic chemicals and altering explicit root exudates such as amino acids and polysaccharides (Abbasi et al., 2014). *P. fluorescens* isolates increased defense enzymes in tomatoes resistant to RKN (Kavitha et al., 2013). In comparison with the control, the application of *P. fluorescens* and *Paecilomyces lilacinus* resulted in low nematode community in roots, tubers and soils (Mohan et al., 2017).

According to Jha et al. (2015), losses resulting from post-fresh fruit and vegetable harvest in India ranged between 4.6% and 15.9%. Although fungicides can inhibit the growth of phytopathogens, their use causes problems to the environment as

well as the human and animal health (Nunes, 2012). The most environmentally acceptable practice to control post-harvest fungal diseases is by using BCAs. In general, BCAs can protect plants from fungal diseases, and are currently a viable option to manage post-harvest diseases associated with plant pathogens (Ghazanfar et al., 2016). In agriculture, BCAs can offer a number of advantages, including the reduction in the causing agents, farming preservation, minimum labor, soil, water plant contamination, and waste management difficulties (Torres et al., 2016). Fungal species, such as *Alternaria*, *Aspergillus*, *Penicillium*, and *Fusarium* producing mycotoxins, are harmful to green vegetables and cause post-harvest diseases. Mycotoxins, such as fumonisin, ochratoxins, aflatoxins and other toxins, are released in vegetables and fruits infected with the fungal pathogens, *Fusarium*, *Alternaria*, and *Aspergillus* (Sanzani et al., 2016). The use of biopriming and pelletizing techniques of *Serratia plymuthica* HRO-C48 alongside *Verticillium dahliae* in canola plants revealed a significant

biocontrol (Muller and Berg, 2008); thus, providing evidence of the ability of BCAs to manage diseases comparable to chemical fungicides.

Bacillus spp. produce a variety of compounds involved in the biocontrol of phytopathogens on various plants, including potato, rice, tomato, wheat, groundnut, brinjal, chickpea, and cucumber (Peng et al., 2014). *Bacillus* sp. BS061 isolate can mitigate the effect of *Botrytis cinerea* to reduce the occurrence of gray mold and powdery mildew diseases in strawberry and cucumber (Kim et al., 2013). Park et al. (2013) found that *Pectobacterium carotovorum* SCC1 can manage soft rot disease in tobacco plants when conjugated with *B. subtilis* strain B4 and BTH fungicides. The root-knot and root rot pathogens are often suppressed when *Pseudomonas* spp. are used as BCAs (Habiba et al., 2016). Farhat et al. (2017) revealed that PGPR isolates had antifungal activities in mungbean plants against *Rhizoctonia solani*, *Macrophomina phaseolina*, *F. solani*, and *F. oxysporum*. These isolates can also be used to prevent fungal infections that cause root rot disease. The application of the bacterial BCA, *Pseudomonas aeruginosa*, can manage anthracnose in the chili pepper against the causal pathogen *Colletotrichum capsici* (Jisha et al., 2018). *P. aeruginosa* can also induce systemic resistance of chili pepper to anthracnose.

Synthetic chemical pesticides are mainly used for post-harvest disease management. Thus, this may lead to plant pathogen resistance, soil deterioration, and toxicological hazards for the humans and the environment. Nowadays, a general trend, as a result, has been shifted toward finding an alternative to the use of agrochemicals in plant disease management. Compared to synthetic chemical fungicides, the use of microbial antagonists or BCAs has become a “hot” topic due to the numerous advantages as non-hazardous, green, economical and feasible applications to control post-harvest pathogen infections (Bonaterra et al., 2012).

Fungi as BCAs

Fungal BCAs are able to antagonize plant pathogens and protect their host plants. For example, several strains of *Trichoderma* have been developed as BCAs against the fungal pathogens *Penicillium*, *Fusarium*, *Aspergillus*, *Alternaria*, *Pythium*, *Rhizoctonia*, *Phytophthora*, *Pyricularia*, *Botrytis*, and *Gaeumannomyces* (Pal and Gardener, 2006; Adebola and Amadi, 2010; Agarwal et al., 2011; Alam et al., 2011; Nally et al., 2012). As a BCA, *Trichoderma* can suppress various air- and soil-borne plant pathogens; thus, can be conceivably used as biopesticides in greenhouse and/or field trials. According to Silva et al. (2017), certain strains of nematophagous fungi can manage the populations of *Meloidogyne enterolobii* in an integrated pest management (IPM) approach. AMF could also protect crops against soil-borne pathogens, including RKN, albeit the unclear mechanisms of antagonism (Vos et al., 2012).

The use of nematophagous and endoparasitic fungi has been deployed as antagonists to suppress RKN (Pendse et al., 2013). The talc-based formulation of the fungal BCA, *Paecilomyces lilacinus*,

was found to be more active in reducing the population of *Meloidogyne incognita* in soils cultivated with tomato plants (Priya and Kumar, 2006). The efficiency of *P. lilacinus* in controlling nematodes was observed in several horticultural crops, including tomato, okra, and capsicum (Rao, 2007). The most widely used BCA for plant-parasitic nematodes is the fungus *P. lilacinus*, which has shown an appropriate replacement to synthetic chemical control in pre- and post-planting applications (Atkins et al., 2005). *P. lilacinus* infects eggs, juveniles and females of *M. javanica* by direct hyphal penetration (Esfahani and Pour, 2006). *P. lilacinus* can boost tomato yield while reducing the population of *M. incognita* in the soil and on the roots (Kalele et al., 2010). RKN management can also be achieved by using *P. lilacinus* and *Bacillus firmus* either individually or in combination. However, the mixture of *P. lilacinus* and *B. firmus* applied in soils 2 weeks prior to tomato transplantation showed the best practice to control *Meloidogyne* spp. (Anastasiadis et al., 2008).

Coating the seed with *Trichoderma viride* and *P. lilacinus* effectively reduced the nematode population in the soil. Species of *Aspergillus* and *Paecilomyces* were found to be antagonistic to *M. incognita* when compared to the single bio-agent treatment; thus, resulting in enhanced plant growth (Table 1; Bontempo et al., 2017). Kerry and Hidalgo-Diaz (2004) developed a management technique using the nematophagous fungus *Pochonia chlamydosporia* to manage RKN for the purpose of organic vegetable production. Okra seeds treated with *Trichoderma harzianum*, *T. viride*, *P. lilacinus*, *P. chlamydosporia*, and *P. fluorescens* at 20 g kg⁻¹ seed significantly reduced the nematode population in the soil and promoted plant growth development (Kumar et al., 2012). Sharf et al. (2014) have reported that *P. chlamydosporia* exhibited nematocidal effects against *M. incognita* on infected common bean under greenhouse condition. *Trichoderma* spp. synthesizing chitinases, lytic enzymes, proteases, and glucanases were found to manage vegetable crop diseases (Punja and Utkhede, 2003). *T. harzianum*, *T. viride*, and *T. hamatum* have nematocidal properties when they colonize the roots of host plant and enhance their growth performance (Girlanda et al., 2001; Siddiqui and Shaukat, 2004; Zhang and Zhang, 2009). Because crop yield is mainly influenced by climatic conditions, agronomic factors, pests, and nutrient availability in the soil (Harman et al., 2004; Elrys et al., 2019a, 2020a), researchers must consider these factors in the selection of fungal BCAs.

Likewise, *Trichoderma* spp. can prevent nematode penetration and development in plants through the regulation of metabolites (Bokhari, 2009). Usman and Siddiqui (2012) have shown that the *M. incognita* and other RKN are more affected by the culture filtrate of *Trichoderma*. Species of *Trichoderma* can produce viridin, a nematocidal chemical (Watanabe et al., 2004). Gliotoxin and acetic acid, have also been reported as nematocidal substances in the culture filtrates of *T. virens* and *T. longibrachiatum*, respectively (Anitha and Murugesan, 2005). In response to *M. incognita*, *T. polysporum* has the ability to synthesize cyclosporine, the peptide that has a nematocidal action (Li et al.,

2007). The efficacy of *P. lilacinus*, as bioagents or bioproducts in mixtures, significantly decreased the number of *M. incognita* on eggplant (Hanawi, 2016). It has been shown that different sources of N and carbon affect the growth and antagonism of *Trichothecium roseum* and *T. viride* (Arya, 2011). Although fructose and lysine were mostly effective against *T. viride*, rhamnose and glycine were more effective against *T. roseum*. There is an adverse effect of fungal culture filtrates on the egg hatching and juvenile mortality of RKN. Plants treated with the fungal BCA, *Lecanicillium muscarium*, decreased the number of galls in plants, eggs, juveniles (J2) and the reproduction factor (Rf) of *Meloidogyne hapla* compared to control plants (Hussain et al., 2017). In addition, plant growth was greatly improved when treated with *L. muscarium*. *Trichoderma* and *P. lilacinum* isolates dramatically reduced nematode egg number and mass, minimized root gal injury, and improved plant root mass development when compared to control plants without the fungal BCAs (Kiriga et al., 2018). Overall, more than 30 genera and 80 species of fungi can parasitize RKN (Gaziea-Soliman et al., 2017). Prince et al. (2011) have demonstrated that the fungus, *Colletotrichum falcatum*, has antagonistic potential against the fungal pathogens *Penicillium citrinum*, *Botrytis cinerea*, and *Trichoderma glaucum*. Moreover, other fungi, such as *Ampelomyces speciosus* and *Acremonium alternatum*, have the ability to degrade the mycelia of fungal pathogens, indicating that not only rhizobacteria, but also fungi can serve as BCAs (Kiss, 2003).

Mechanisms used by MBCAs

Understanding the appropriate conditions for implementing proper programs against plant pathogens requires collaborations between different research groups focusing on the mechanisms associated with MBCAs to manage diseases on plants. In the last two decades, extensive research has focused on the antifungal effect, rhizosphere colonization, and crop benefits linked to MBCA (Compant et al., 2010; Al Hamad et al., 2021; Al Raish et al., 2021; Alwahshi et al., 2022). Thus, the products of MBCA on plant fungal pathogens and their impacts on plants are illustrated in Figure 2. The primary strategy of MBCA are summarized as antibiosis, competition for micronutrients such as iron, mycoparasitism, production of hydrolytic enzymes, and induction of ISR in host plants (Figure 3). In addition, the production of metabolites that are inhibitory to plant pathogenic rhizosphere microorganisms is considered one of the major biocontrol activities in many MBCA (Haas and Keel, 2003).

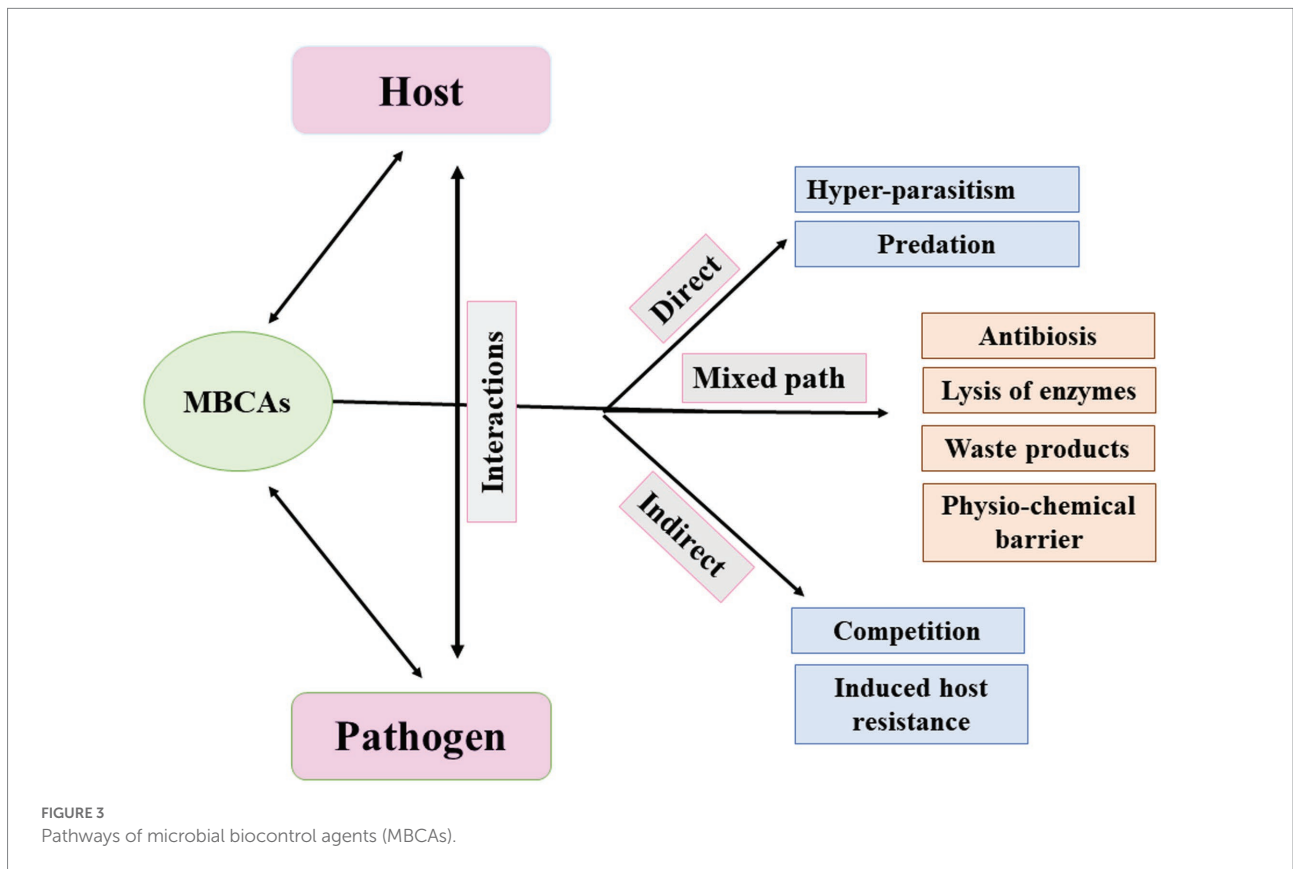
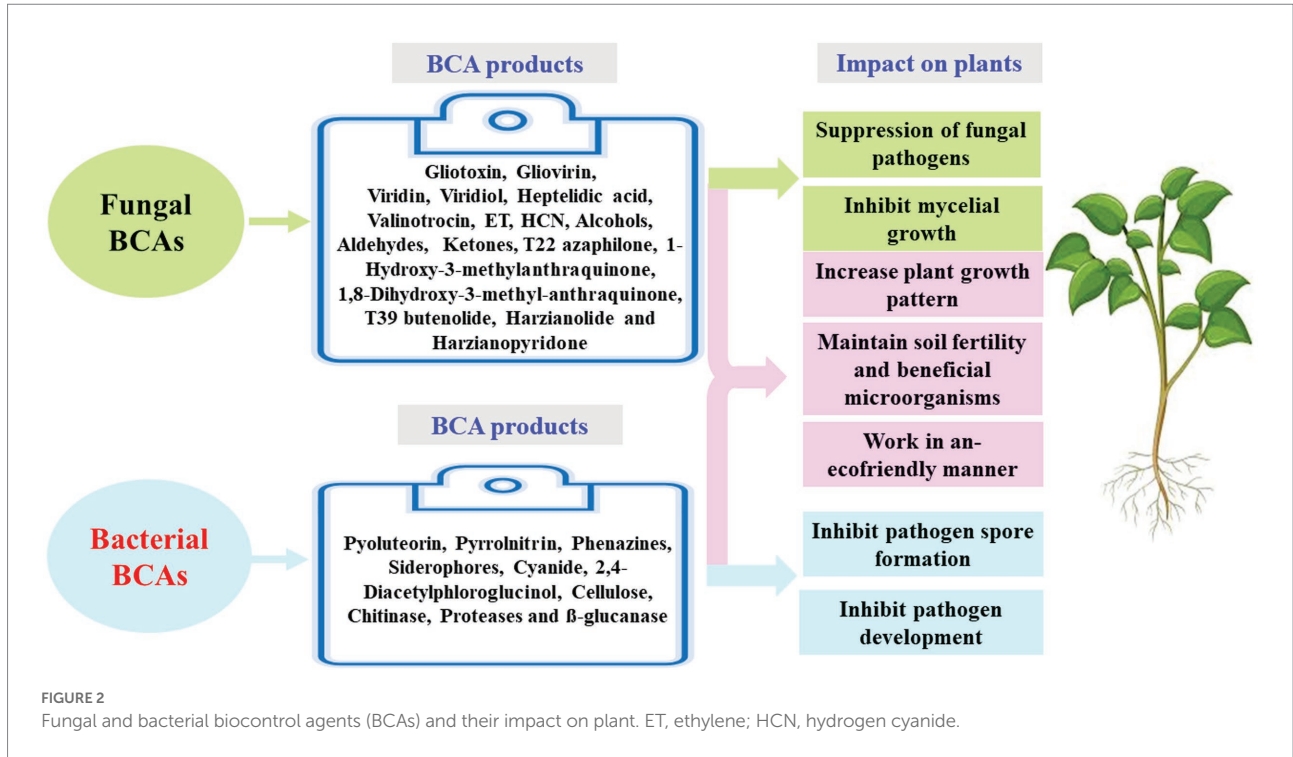
In several microorganisms, antibiosis, also known as secondary metabolites, results in the production of various toxic chemicals to pathogenic microorganisms; thus, they are suitable for the plant growth and development. An antibiotic-producing microorganism must manufacture the antibiotic in the correct microniche on the root surface to effectively control plant diseases (Lugtenberg and Kamilova, 2009). Actinobacteria (8,700 distinct

antibiotics), bacteria (2,900), and fungi (4,900) can produce massive amounts of antibiotics (Bérdy, 2005). Mutagenesis has been reported to be successful in determining the role of antibiotics generated by bacterial BCA isolates to control pathogens associated with plant infections (Liu et al., 2007).

Ongena and Jacques (2008) have investigated the lipopeptides (surfactin, iturin, and fengycin) in *Bacillus* spp. It has also been reported that pyrrolnitrin, 2,4-diacetylphloroglucinol (DAPG), and phenazine can be potential antibiotic metabolites in *Pseudomonas* (Raaijmakers and Mazzola, 2012). *Pseudomonas* spp. have the ability to generate pyoluteorin, siderophores, and cyanide, among other antimicrobial chemicals (Compant et al., 2010). In addition, the enzymatic activity of cellulase, proteases, β -glucanase, and chitinase can lyse fungal cells (Hernandez-Leon et al., 2015). Antibiotic metabolites produced by *Pseudomonas* spp. are regulated by complex regulatory networks and high number of transcription factors (Berry et al., 2014). Significant classes of antifungal antibiotics are lipopeptides or peptides that are produced by the ribosomes or non-ribosomes of *Bacillus* spp. (Figure 2). Arseneault and Filion (2017) have discussed that antibiotics can be generated by BCA strains in soil.

Bacillus spp. have the ability to produce various biologically active chemicals that hinder the development of several crop diseases (Zhao et al., 2013). An investigation by Chowdhury et al. (2015) revealed that the quantity of antibacterial or antifungal chemicals produced by *Bacillus* spp. in the rhizosphere is somewhat little, causing doubts on the role of rapid management of plant diseases. Several isolates of *P. fluorescens* were found to generate cyclic lipopeptides (CLPs), such as viscosinamide, amphisin and tensin, that were effective against fungal pathogens, *R. solani* and *Pythium ultimum* (Nielsen et al., 2002).

Biological control is an application of beneficial organisms, genes, and their products in the form of metabolites (Glare et al., 2012). Several *in vitro* metabolites of microorganisms were utilized to control pathogenic infections (Köhl et al., 2019). As a result, these secondary metabolites can be utilized as products of a BCA; and thus, they are effective to ameliorate the negative impact of other pathogenic microorganisms while also being environmentally friendly. Antimicrobial activities of some fungal BCAs may also exhibit antagonistic effects against fungi. For example, *Trichoderma* spp. are commonly found in soil and provide a variety of volatile and nonvolatile compounds. Volatile compounds, such as cyanide, hydrogen, ET, aldehydes, ketones and alcohols; and nonvolatile substances, such as peptides, can inhibit the mycelial growth in some pathogenic fungi. Many antifungal compounds, such as gliovirin, gliotoxin, viridiol, heptelidic acid, valinotrocin, and viridin can be produced by *Gliocladium virens*, which acts as a MBCA. Singh et al. (2005) demonstrated that gliotoxin can effectively reduce the fungal pathogens, *Pythium aphanidermatum*, *M. phaseolina*, *Pythium debaryanum*, *R. solani*, *Sclerotium rolfsii*, and *Rhizoctonia bataticola*. Vinale et al. (2009) have stated that the production of 1-hydroxy-3-methylanthraquinone, 1,8-dihydroxy-3-methylanthraquinone, T22 azaphilone, harzianolide, T39butenolide, and



harzianopyridone by *T. harzianum* strains T22 and T39 has the ability to control the plant fungal pathogens *Leptosphaeria maculans*, *Phytophthora cinnamomi*, *R. solani*, *Botrytis cinerea*,

and *P. ultimum*. Several secondary metabolites have been isolated and recognized by different methods such as high-performance liquid chromatography (HPLC) and gas chromatography–mass

spectrometry (GC-MS). [Shanthiyaa et al. \(2013\)](#) have investigated three isolates, Cg-5, Cg-6, and Cg-7, that produce the secondary metabolite, chaetoglobosin A, in the culture filtrate detected by the UV spectrum at 250 nm. The antimicrobial compounds released by fungi may also control phytopathogens during post-harvest infections. The post-harvest infection causes excessive damages in vegetables and fruit ([Figures 4, 5](#)).

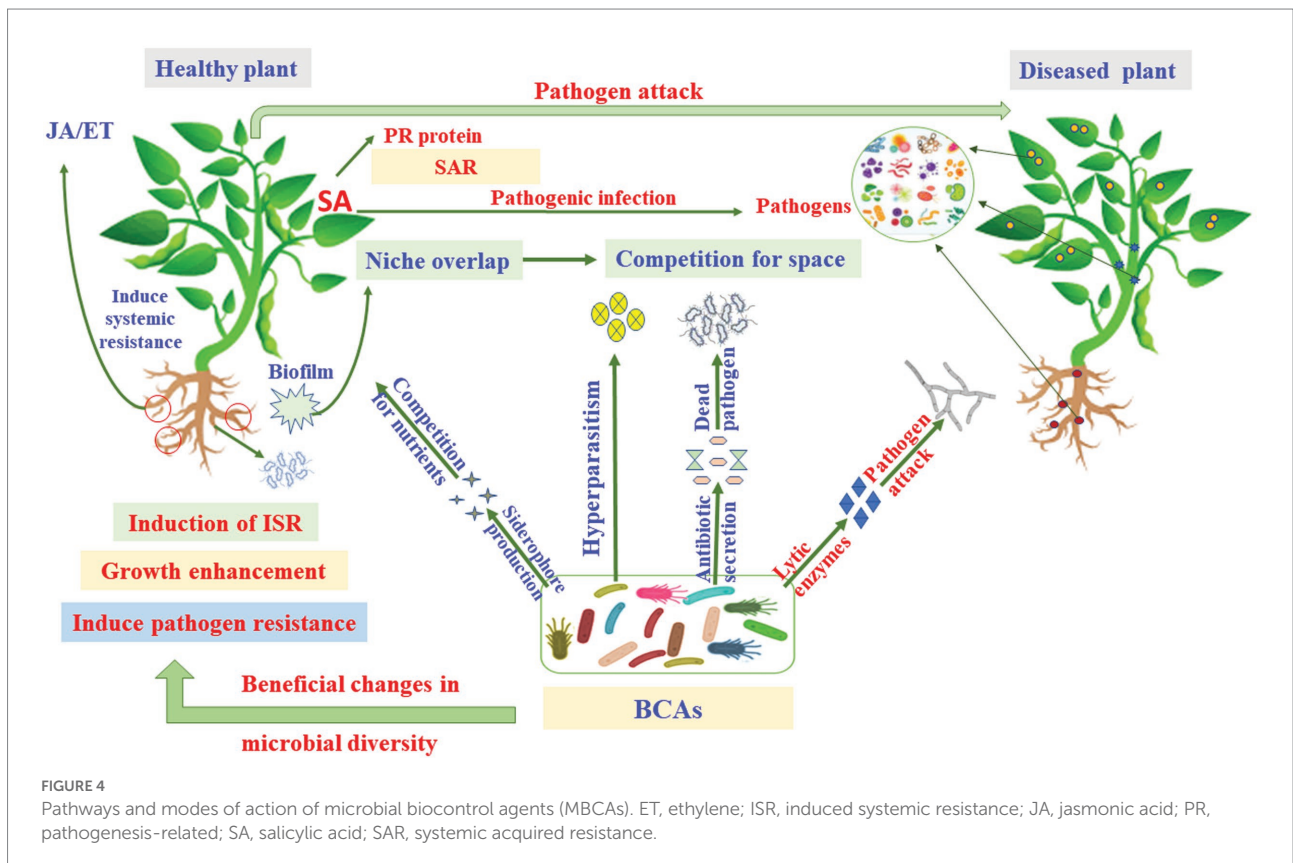
Competition in the rhizosphere

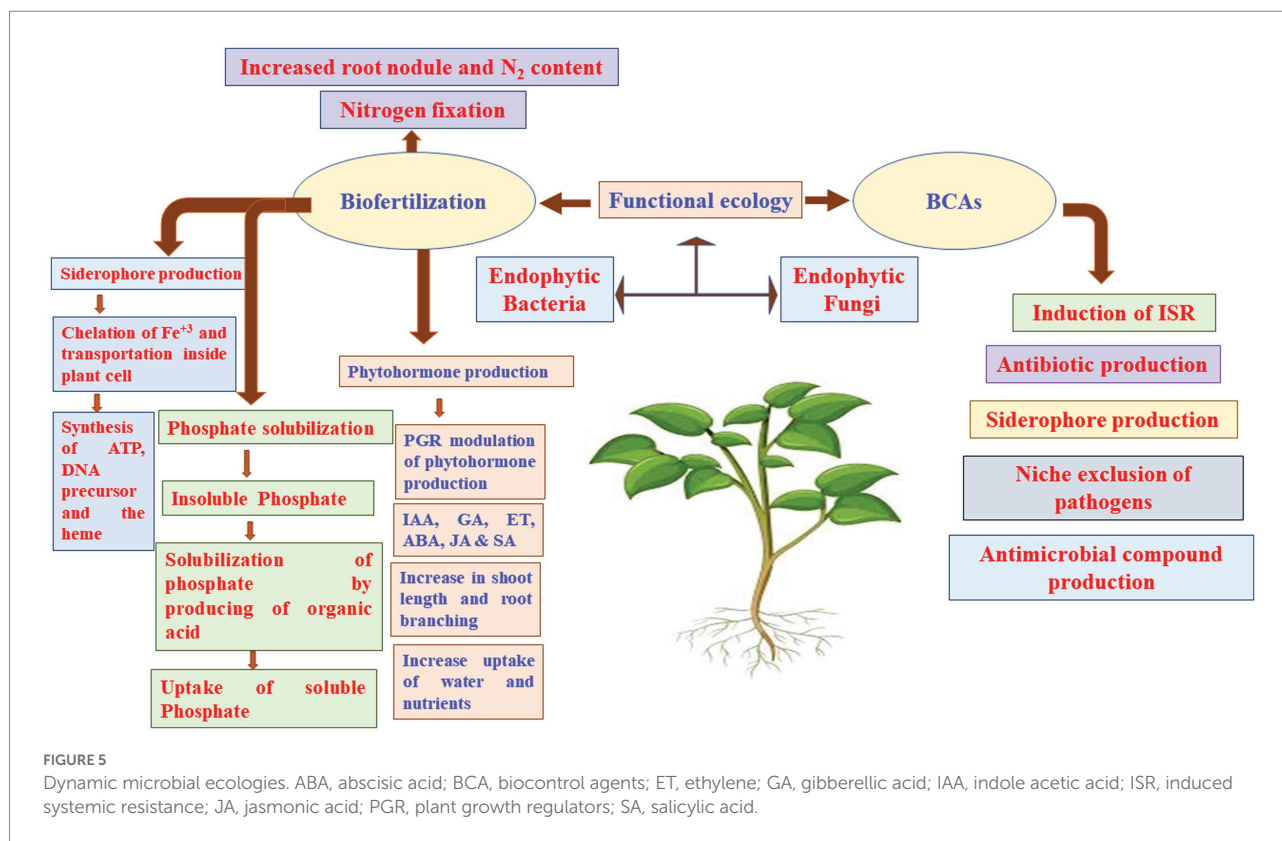
Co-existence of two living microorganisms occurs when a population of a particular microorganism strives to achieve something greater, such as space or food supply ([Stirling, 2017](#)). Pathogenic and non-pathogenic microorganisms compete for food and resources in the rhizosphere. It has been known for a long time that non-pathogenic plant-associated bacteria are usually protected by colonizing plants and, as a result, this debilitate the limited available substrates and prevent the spread of the pathogens. The abilities of any microorganism to compete with others for essential nutrients and exudates secreted by the plant roots and their capability of colonizing into the root surface of host plants are termed rhizosphere competence. In the rhizosphere, the beneficial interactions between plants and microorganisms can regularly occur; thus, promoting growth and/

or enhancing tolerance to biotic and abiotic stresses in plants ([Zamioudis and Pieterse, 2012](#)).

Rhizosphere competence can successfully establish microbial communities on or near the plant roots. Plant root colonization by PGPM can protect plants against pathogens and promote plant growth, and chemotaxis to root exudates is considered as an essential prerequisite for efficient root colonization ([de Weert and Bloemberg, 2006](#)). Microbial community in the rhizosphere is found to be important shortly after planting, but regularly decreases during the cropping season ([Weller, 2007](#)). [Adesina et al. \(2009\)](#) have reported *in vitro* antagonism of 15 *Pseudomonas* strains to *R. solani* in the rhizosphere. Only *Pseudomonas jessenii* RU47 has been effective to bottom rot disease on lettuce caused by *R. solani*. Tryptophan can stimulate the growth of adventitious roots and root hairs of the IAA-producing *B. subtilis* SRB28, which can colonize root tissues in sorghum, produce microcolonies, and persist in the rhizosphere ([Das et al., 2010](#)).

Rhizosphere microorganisms promoting plant growth, represent a wide range of species. PGPM are categorized according to their ability to colonize roots, survive, increase their numbers in the microhabitats on the root surface, compete with indigenous microorganisms, and increase resistance in host crops ([Gamalero et al., 2004](#)). PGPM can not only promote plant development, but also they are often used as BCAs to suppress plant diseases. The plant-associated *Bacillus*, *Pseudomonas*, *Lactobacillus* and actinobacteria strains are used as biofertilizers





and BCAs in agriculture (Borriss, 2011; Sivasakthi et al., 2014; Lamont et al., 2017; Shivilata and Satyanarayana, 2017). Furthermore, *Acetobacter*, *Serratia*, *Azospirillum*, *Paenibacillus Burkholderia*, *Herbaspirillum*, and *Rhodococcus* can also enhance growth in crop plants (Babalola, 2010). Chakraborty et al. (2013) reported that a number of PGPR traits, such as production of siderophore, solubilization of phosphate, synthesis of IAA, and antagonism against fungal pathogens, were found to stimulate growth in tea plants. This has been linked with an increase in the number of shoots and leaves under greenhouse and field conditions. In general, soils with active microbial ecosystems and high organic matter require less fertilizer than soils without any microorganisms (Bender et al., 2016).

Biofertilizers made from microorganisms that help plants obtain their nutrients can colonize plant roots, to solubilize P, produce siderophore and HCN, and fix N₂ (Figure 5; Pii et al., 2015; El-Sobky et al., 2022). N₂ fixation by PGPR provides a considerable amount of N to the farming systems worldwide, with estimations ranging from 20 to 22 Tg N annually (Herridge et al., 2008), which may reach in some years to up to 40 Tg N (Galloway et al., 2008). Moreover, it has been reported that the biological N₂ fixation may provide the African countries approximately 12 Tg N year⁻¹ (Elrys et al., 2019b, 2020b). Crop yields might be limited by other nutritional elements, such as Fe and Zn. Similar to P, Fe is highly abundant in soils; yet, it is not available to plants in most cases. The synthesis of organic acids or siderophores by various PGPR strains increases Fe accessibility (Ahmed and Holmstrom, 2014).

Auxins are produced by a variety of PGPR (Gupta et al., 2015) that is involved in plant growth and development (Jha and Saraf, 2015) and plant architecture (Vacheron et al., 2013). The auxin, IAA, produced by PGPR has received much of attention. It is highly involved during PGPR-plant interactions (Afzal et al., 2015). Auxin-producing PGPR have been reported to cause transcriptional alterations in the hormone levels, resistance/tolerance to biotic/abiotic stress, and regulation of cell wall-linked genes (Spaepen et al., 2014). IAA may also increase root length (Hong et al., 1991), enhance root biomass, while reducing the size and density of stomata (Llorente et al., 2016). Plant growth and development can also be stimulated by the induction of auxin-response genes (Ruzzi and Aroca, 2015).

In addition, PGPRs can produce GA and CKs (Gupta et al., 2015), although the exact process remains unknown (Kang et al., 2009). A limited number of PGPR strains can produce huge amounts of GA; thus, significantly increase the shoot growth in plants (Jha and Saraf, 2015). Exudates are expected to contain organic acids, sugars, and amino acids, which are highly abundant in the cytoplasm of plants, but low quantities of complex secondary metabolites, including flavonoids, terpenes, and phenolic substances, which may attract certain rhizosphere microorganisms (Musilova et al., 2016). Plant health and physiology could be improved due to PGPR colonization of roots, resulting in more seeds and blooms (Kumar et al., 2016). According to Nivedhitha et al. (2008), actinobacteria isolated from the rhizosphere of bamboo was found to be capable to

suppress the fungal pathogen, *Fusarium* sp., while boosting plant growth and development. Harzianic acid produced by *T. harzianum* not only promoted plant growth, but also showed antifungal effects against *Pythium irregulare*, *Sclerotinia sclerotiorum*, and *R. solani*, even at very low doses (Vinale et al., 2009). MBCA are important to the advancement and improvement of plant growth development, as well as the prevention of the attack of plant pathogens.

Future perspectives

Biological control management is one of the most promising applications for sustainable agriculture. It is a proven to be eco-friendly agricultural pest control approach. This strategy uses living microorganisms to reduce the pest populations in a conservative, dependable, and ecologically amicable manner. In the developed countries, biological control is a remarkable tool to achieve sustainable, less expensive, and safe pest control management; thus, offering benefits to breeders and consumers when compared to synthetic (chemical) pest management. This review has provided an overview of antagonistic modes of action of MBCA, which are regarded as practical substitutions to synthetic fungicides as well as stimulation of plant growth and development for post-harvest purposes. Researchers working in the field of MBCA must anticipate new and distinct questions, in order to provide solutions that help in the development of novel biocontrol technologies/applications. Bioinformatics, molecular biology, analytical chemistry, and biostatistics have also shed lights on new research areas aimed at defining the MBCA-pathogen-plant interaction (Spadaro and Gullino, 2005).

One should not neglect the environmental conditions that also play a crucial role in the process of antagonism and the mode(s) of action of MBCA. The following conditions should be taken into consideration, when researchers isolate, identify and characterize a MBCA strain:

1. The spread of the infection associated with nematodes, fungi, and bacteria, as well as the potential antagonists in the micro- and macro-environment of the interaction.
2. The best conditions for the application of BCA.
3. The reaction of MBCA to the local communities and to various management strategies.
4. The limiting factors of effective colonization and articulation of biological control characteristics.
5. The plant components and dynamics that induce host defense.

Conclusion

Many crops are affected by various pathogens. PGPM of pests and diseases in crops are generally regarded as a sustainable alternative for conventional chemical plant protection. These

PGPR and PGPF acting as MBCAs are a safe, effective, and environmentally friendly form of pest management that do not harm the environment or the human health. PGPR/PGPF are antagonistic microorganisms that could be exploited as biopesticides and biofertilizers for better plant health and growth improvement. Adoption of PGPR/PGPF-based biopesticides/biofertilizers on a commercial scale may substantially contribute to sustainable agriculture and safe environment. This review has provided an overview on the research related to PGPMs, their benefits and effects as potential bioinoculants for plant growth and biological control. The increased use of PGPMs requires the achievement of accurate selection of beneficial PGPR/PGPF strains and consortia, the mechanisms underlying PGPM-plant interactions, and the ability to prepare for future agricultural challenges.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

- Abbas, R., Rasul, S., Aslam, K., Baber, M., Shahid, M., Mubeen, F., et al. (2019). Halotolerant PGPR: a hope for cultivation of saline soils. *J. King Saud Univ. Sci.* 31, 1195–1201. doi: 10.1016/j.jksus.2019.02.019
- Abbasi, M. W., Ahmed, N., Zaki, M. J., Shaikat, S. S., and Khan, D. (2014). Potential of *Bacillus* species against *Meloidogyne javanica* parasitizing eggplant (*Solanum melongena* L.) and induced biochemical changes. *Plant Soil* 375, 159–173. doi: 10.1007/s11104-013-1931-6
- Abd El-Mageed, T. A., Rady, M. M., Taha, R. S., Abd El Azeam, S., Simpson, C. R., and Semida, W. M. (2020). Effects of integrated use of residual sulfur-enhanced biochar with effective microorganisms on soil properties, plant growth and short-term productivity of *Capsicum annuum* under salt stress. *Sci. Hortic.* 261:108930. doi: 10.1016/j.scienta.2019.108930
- Abriouel, H., Franz, C. M. A. P., Omar, N. B., and Gálvez, A. (2011). Diversity and applications of *Bacillus* bacteriocins. *FEMS Microbiol. Rev.* 35, 201–232. doi: 10.1111/j.1574-6976.2010.00244.x
- AbuQamar, S. F., Moustafa, K., and Tran, L. S. (2017). Mechanisms and strategies of plant defense against *Botrytis cinerea*. *Crit. Rev. Biotechnol.* 37, 262–274. doi: 10.1080/07388551.2016.1271767
- Adebola, M. O., and Amadi, J. E. (2010). Screening three *Aspergillus* species for antagonistic activities against the cocoa black pod organism (*Phytophthora palmivora*). *Agric. Biol. J. North Am.* 1, 362–365. doi: 10.5251/abjna.2010.1.3.362.365
- Adesina, M. F., Grosch, R., Lembke, A., Vatchev, T. D., and Smalla, K. (2009). *In vitro* antagonists of *Rhizoctonia solani* tested on lettuce: rhizosphere competence, biocontrol efficiency and rhizosphere microbial community response. *FEMS Microbiol. Ecol.* 69, 62–74. doi: 10.1111/j.1574-6941.2009.00685.x
- Afzal, I., Shinwari, Z. K., and Iqar, I. (2015). Selective isolation and characterization of agriculturally beneficial endophytic bacteria from wild hemp using canola. *Pak. J. Bot.* 47, 1999–2008.
- Agarwal, T., Malhotra, A., Trivedi, P. C., and Biyani, M. (2011). Biocontrol potential of *Gliocladium virens* against fungal pathogens isolated from chickpea, lentil and black gram seeds. *Int. J. Agric. Technol.* 7, 1833–1839.
- Agbor, C., Djeani, A. C., Muyang, R. F., and Mbouobda, H. D. (2021). *Rhizopus* spp. promoting and inducing late blight (*Phytophthora infestans*) resistance in *Solanum lycopersicum* L. *Annu. Res. Rev. Biol.* 36, 1–13. doi: 10.9734/arrb/2021/v36i230338
- Ahmed, E., and Holmstrom, S. J. (2014). Siderophores in environmental research: roles and applications. *J. Microbiol. Biotechnol.* 7, 196–208. doi: 10.1111/1751-7915.12117
- Al Hamad, B. M., Al Raish, S. M., Ramadan, G. A., Saeed, E. E., Alameri, S. S. A., Al Senaani, S. S., et al. (2021). Effectiveness of augmentative biological control of *Streptomyces griseorubens* UAE2 depends on 1-aminocyclopropane-1-carboxylic acid deaminase activity against *Neoscytalidium dimidiatum*. *J. Fungi.* 7:885. doi: 10.3390/jof7110885
- Al Raish, S. M., Saeed, E. E., Alyafei, D. M., El-Tarabily, K. A., and AbuQamar, S. F. (2021). Evaluation of streptomycete actinobacterial isolates as biocontrol agents against royal poinciana stem canker disease caused by the fungal pathogen *Neoscytalidium dimidiatum*. *Biol. Control* 164:104783. doi: 10.1016/j.biocontrol.2021.104783
- Alam, S. S., Sakamoto, K., Amemiya, Y., and Inubushi, K. (2011). Biocontrol efficiency of *Fusarium* wilt diseases by a root-colonizing fungus *Penicillium* sp. *Soil Sci. Plant Nutr.* 57, 204–212. doi: 10.1080/00380768.2011.564996
- Alblooshi, A. A., Purayil, G. P., Saeed, E. E., Ramadan, G. A., Tariq, S., Altaee, A. S., et al. (2022). Biocontrol potential of endophytic actinobacteria against *Fusarium solani*, the causal agent of sudden decline syndrome on date palm in the UAE. *J. Fungi.* 8:8. doi: 10.3390/jof8010008
- Al-Hussini, H. S., Al-Rawahi, A. Y., Al-Marhoon, A. A., Al-Abri, S. A., Al-Mahmooli, I. H., Al-Sadi, A. M., et al. (2019). Biological control of damping-off of tomato caused by *Pythium aphanidermatum* by using native antagonistic rhizobacteria isolated from Omani soil. *J. Plant Pathol.* 101, 315–322. doi: 10.1007/s42161-018-0184-x
- Alwahshi, K. J., Purayil, G. P., Saeed, E. E., Abufarajallah, H. A., Aldhaheri, S. J., AbuQamar, S. F., et al. (2022). The ACC deaminase-producing *Streptomyces violaceoruber* UAE1 can provide further protection from sudden decline syndrome on date palm. *Front. Plant Sci.* 13:904166. doi: 10.3389/fpls.2022.904166
- Anastasiadis, I. A., Giannakou, I. O., Prophetou-Athanasiadou, D. A., and Gowen, S. R. (2008). The combined effect of the application of a biocontrol agent *Paecilomyces lilacinus*, with various practices for the control of root-knot nematodes. *Crop Prot.* 27, 352–361. doi: 10.1016/j.cropro.2007.06.008
- Anitha, R., and Murugesan, K. (2005). Production of gliotoxin on natural substrates by *Trichoderma virens*. *J. Basic Microbiol.* 45, 12–19. doi: 10.1002/jobm.200410451
- Antoun, H., and Kloepper, J. (2001). “Plant growth promoting rhizobacteria,” in *Encyclopedia of genetics*. eds. S. Brenner and J. H. Miller (New York: Academic Press), 1477–1480.
- Arseneault, T., and Filion, M. (2017). Biocontrol through antibiosis: exploring the role played by subinhibitory concentrations of antibiotics in soil and their impact on plant pathogens. *Can. J. Plant Pathol.* 39, 267–274. doi: 10.1080/07060661.2017.1354335
- Arya, R. (2011). Effect of culture filtrates of *Trichoderma viridae* and *Trichothecium roseum* grown on different carbon and nitrogen sources on hatching and mortality of root-knot nematode (*Meloidogyne incognita*). *Indian J. Nematol.* 41, 62–70.
- Ashajyothia, M., Kumara, A., Sheorana, N., Ganesana, P., Gogoia, R., Subbaiyanb, G. K., et al. (2020). Black pepper (*Piper nigrum* L.) associated endophytic *Pseudomonas putida* BP25 alters root phenotype and induces defense in rice (*Oryza sativa* L.) against blast disease incited by *Magnaporthe oryzae*. *Biol. Control* 143. doi: 10.1016/j.biocontrol.2019.104181
- Atkins, S. D., Clark, I. M., Pande, S., Hirsch, P. R., and Kerry, B. K. (2005). The use of real-time PCR and species-specific primers for the identification and monitoring of *Paecilomyces lilacinus*. *FEMS Microbiol. Ecol.* 51, 257–264. doi: 10.1016/j.femsec.2004.09.002
- Babalola, O. O. (2010). Beneficial bacteria of agricultural importance. *Biotechnol. Lett.* 32, 1559–1570. doi: 10.1007/s10529-010-0347-0
- Barratt, B. I. P., Moran, V. C., Bigler, F., and van Lenteren, J. C. (2018). The status of biological control and recommendations for improving uptake for the future. *Biol. Control* 63, 155–167. doi: 10.1007/s10526-017-9831-y
- Bashan, Y., de Bashan, L. E., Prabhu, S. R., and Hernandez, J. -P. (2014). Advances in plant growth-promoting bacterial inoculant technology: formulations and practical perspectives (1998–2013). *Plant Soil* 378, 1–33. doi: 10.1007/s11104-013-196-x
- Begum, M., Lees, E., Ampt, P., and Mansfield, S. (2017). Development of Australian commercial producers of invertebrate biological control agents from 1971 to 2014. *Biol. Control* 62, 525–533. doi: 10.1007/s10526-017-9822-z
- Bender, S. F., Wagg, C., and Van Der Heijden, M. G. A. (2016). An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability. *Trends Ecol. Evol.* 31, 440–452. doi: 10.1016/j.tree.2016.02.016
- Beneduzi, A., Ambrosini, A., and Passaglia, L. M. P. (2012). Plant growth promoting rhizobacteria (PGPR): their potential as antagonists and biocontrol agents. *Genet. Mol. Biol.* 35, 1044–1051. doi: 10.1590/S1415-47522012000600020
- Bérdy, J. (2005). Bioactive microbial metabolites. *J. Antibiot.* 58, 1–26. doi: 10.1038/ja.2005.1
- Berger, B., Patz, S., Ruppel, S., Dietel, K., Faetke, S., Junge, H., et al. (2018). Successful formulation and application of plant growth-promoting *Kosakonia radicincitans* in maize cultivation. *Biomed. Res. Int.* 2018:6439481. doi: 10.1155/2018/6439481
- Berry, C. L., Nandi, M., Manuel, J., Brassinga, A. K. C., Fernando, W. G. D., Loewen, P. C., et al. (2014). Characterization of the *Pseudomonas* sp. DF41 quorum sensing locus and its role in fungal antagonism. *Biol. Control* 69, 82–89. doi: 10.1016/j.biocontrol.2013.11.005
- Bhat, M. A., Kumar, V., Bhat, M. A., Wani, I. A., Dar, F. L., Farooq, I., et al. (2020). Mechanistic insights of the interaction of plant growth-promoting rhizobacteria (PGPR) with plant roots toward enhancing plant productivity by alleviating salinity stress. *Front. Microbiol.* 11:1952. doi: 10.3389/fmicb.2020.01952
- Bhattacharyya, P. N., and Jha, D. K. (2012). Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. *World J. Microbiol. Biotechnol.* 28, 1327–1350. doi: 10.1007/s11274-011-0979-9
- Bilesky-José, N., Maruyama, C., Germano-Costa, T., Campos, E., Carvalho, L., Grillo, R., et al. (2021). Biogenic α -Fe₂O₃ nanoparticles enhance the biological activity of *Trichoderma* against the plant pathogen *Sclerotinia sclerotiorum*. *ACS Sustain. Chem. Eng.* 9, 1669–1683. doi: 10.1021/acssuschemeng.0c07349
- Bokhari, F. M. (2009). Efficacy of some *Trichoderma* species in the control of *Rotylenchulus reniformis* and *Meloidogyne javanica*. *Arch. Phytopathol. Plant Prot.* 42, 361–369. doi: 10.1080/03235400601070520
- Bonaterra, A., Badosa, E., Cabrefiga, J., Frances, J., and Montesinos, E. (2012). Prospects and limitations of microbial pesticides for control of bacterial and fungal pomefruit tree diseases. *Trees* 26, 215–226. doi: 10.1007/s00468-011-0626-y
- Bontempo, A. F., Lopes, E. A., Fernandes, R. H., De Freitas, L. G., and Dallemole-Giaretta, R. (2017). Dose-response effect of *Pochonia chlamydosporia* against *Meloidogyne incognita* on carrot under field conditions. *Revista Caatinga Mossoró.* 30, 258–262. doi: 10.1590/1983-21252017v30n129rc
- Borriss, R. (2011). “Use of plant-associated *Bacillus* strains as biofertilizers and biocontrol agents in agriculture,” in *Bacteria in agrobiology: Plant growth responses*. ed. D. K. Maheshwari (Berlin: Springer), 41–76.
- Carrasco-Espinosa, K., García-Cabrera, R. I., Bedoya-López, A., Trujillo-Roldán, M. A., and Valdez-Cruz, N. A. (2015). Positive effect of reduced aeration rate on growth and stereospecificity of dl-malic acid consumption by *Azospirillum brasilense*: improving the shelf life of a liquid inoculant formulation. *J. Biotechnol.* 195, 74–81. doi: 10.1016/j.jbiotec.2014.12.020

- Chakraborty, U., Chakraborty, B. N., Chakraborty, A. P., Sunar, K., and Dey, P. L. (2013). Plant growth promoting rhizobacteria mediated improvement of health status of tea plants. *Indian J. Biotechnol.* 12, 20–31.
- Chakruno, P., Banik, S., and Sumi, K. (2022). “Important diseases of tea (*Camellia sinensis* L.) and their integrated management,” in *Diseases of Horticultural Crops: Diagnosis and Management*. eds. J. N. Srivastava and A. K. Singh (New York: Apple Academic Press), 119–138.
- Chaloner, T. M., Gurr, S. J., and Bebbler, D. P. (2021). Plant pathogen infection risk tracks global crop yields under climate change. *Nat. Clim. Chang.* 11, 710–715. doi: 10.1038/s41558-021-01104-8
- Cheng, X., Ji, X., Li, J., Qi, W., Ge, Y., and Qiao, K. (2019). Characterization of antagonistic *Bacillus methylotrophicus* isolated from rhizosphere and its biocontrol effects on maize stalk rot. *Phytopathology* 109, 571–581. doi: 10.1094/phyto-07-18-0220-r
- Chiranjeevi, N., Kumar, M. R., Padmodaya, B., Venkateswarlu, N. C., Sudhakar, P., Devi, R. S. J., et al. (2021). Studies on extraction, evaluation of crude metabolite extract from endophytic *Bacillus subtilis* and its mechanistic effect on chickpea dry root rot causing pathogen *Rhizoctonia bataticola* (Taub.) Butler. *Pharma Innov.* 10, 898–905.
- Choudhary, D. K., Sharma, K. P., and Gaur, R. K. (2011). Biotechnological perspectives of microbes in agro-ecosystems. *Biotechnol. Lett.* 33, 1905–1910. doi: 10.1007/s10529-011-0662-0
- Chowdhury, S. P., Hartmann, A., Gao, X., and Borriss, R. (2015). Biocontrol mechanism by root-associated *Bacillus amyloliquefaciens* FZB42: a review. *Front. Microbiol.* 6:780. doi: 10.3389/fmicb.2015.00780
- Compant, S., Clément, C., and Sessitsch, A. (2010). Plant growth-promoting bacteria in the rhizo and endosphere of plants: their role, colonization, mechanisms involved and prospects for utilization. *Soil Biol. Biochem.* 42, 669–678. doi: 10.1016/j.soilbio.2009.11.024
- Compant, S., Duffy, B., Nowak, J., Clément, C., and Barka, E. A. (2005). Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. *Appl. Environ. Microbiol.* 71, 4951–4959. doi: 10.1128/AEM.71.9.4951-4959.2005
- Das, S. N., Sarma, P. V., Neeraja, C., Malati, N., and Podile, A. R. (2010). Members of gamma proteobacteria and bacilli represent the culturable diversity of chitinolytic bacteria in chitin-enriched soils. *World J. Microbiol. Biotechnol.* 26, 1875–1881. doi: 10.1007/s11274-010-0369-8
- De la Cruz-Quiroz, R., Roussos, S., Rodríguez-Herrera, R., Hernandez-Castillo, D., and Aguilar, C. N. (2018). Growth inhibition of *Colletotrichum gloeosporioides* and *Phytophthora capsici* by native Mexican *Trichoderma* strains. *Karbalia Int. J. Mod. Sci.* 4, 237–243. doi: 10.1016/j.kijoms.2018.03.002
- de Weert, S., and Bloemberg, G. V. (2006). “Rhizosphere competence and the role of root colonization in biocontrol” in *Plant-Associated Bacteria*. ed. S. S. Gnanamanickam (Dordrecht: Springer), 317–333.
- Di Francesco, A., and Baraldi, E. (2021). How siderophore production can influence the biocontrol activity of *Aureobasidium pullulans* against *Monilinia laxa* on peaches. *Biol. Control* 152:104456. doi: 10.1016/j.biocontrol.2020.104456
- Donley, N. (2019). The USA lags behind other agricultural nations in banning harmful pesticides. *Environ. Health* 18:44. doi: 10.1186/s12940-019-0488-0
- Duffy, B., Schouten, A., and Raaijmakers, J. M. (2003). Pathogen self-defense: mechanisms to counteract microbial antagonism. *Annu. Rev. Phytopathol.* 41, 501–538. doi: 10.1146/annurev.phyto.41.052002.095606
- Dukarea, A., and Paulb, S. (2021). Biological control of *Fusarium* wilt and growth promotion in pigeon pea (*Cajanus cajan*) by antagonistic rhizobacteria, displaying multiple modes of pathogen inhibition. *Rhizosphere* 17:100278. doi: 10.1016/j.rhisp.2020.100278
- Elnahal, A. S., El-Saadony, M. T., Saad, A. M., Desoky, E. S. M., El-Tahan, A. M., Rady, M. M., et al. (2022). The use of microbial inoculants for biological control, plant growth promotion, and sustainable agriculture: a review. *Eur. J. Plant Pathol.* 162, 759–792. doi: 10.1007/s10658-021-02393-7
- Elrys, A. S., Abdel-Fattah, M. K., Raza, S., Chen, Z., and Zhou, J. (2019b). Spatial trends in the budget of nitrogen flows in the African agro-food system over the past five decades. *Environ. Res. Lett.* 14:124091. doi: 10.1088/1748-9326/ab5d9e
- Elrys, A. S., Abdo, A. I. E., Abdel-Hamed, E. M., and Desoky, E. S. M. (2020a). Integrative application of licorice root extract or lipoic acid with fulvic acid improves wheat production and defenses under salt stress conditions. *Ecotoxicol. Environ. Saf.* 190:110144. doi: 10.1016/j.ecoenv.2019.110144
- Elrys, A. S., Desoky, E. S. M., Abo El-Maati, M. F., Elnahal, A. S., Abdo, A. I., Raza, S., et al. (2019a). Can secondary metabolites extracted from moringa seeds suppress ammonia oxidizers to increase nitrogen use efficiency and reduce nitrate contamination in potato tubers? *Ecotoxicol. Environ. Saf.* 185:109689. doi: 10.1016/j.ecoenv.2019.109689
- Elrys, A. S., Metwally, M. S., Raza, S., Alnaimy, M. A., Shaheen, S. M., Chen, Z., et al. (2020b). How much nitrogen does Africa need to feed itself by 2050? *J. Environ. Manage.* 268:110488. doi: 10.1016/j.jenvman.2020.110488
- El-Sobky, E. -S. E. A., Taha, A. E., El-Sharnouby, M., Sayed, S. M., and Elrys, A. S. (2022). Zinc-biochemical co-fertilization improves rice performance and reduces nutrient surplus under semi-arid environmental conditions. *Saudi J. Biol. Sci.* 29, 653–1667. doi: 10.1016/j.sjbs.2021.10.066
- Esfahani, N. M., and Pour, B. A. (2006). The effects of *Paecilomyces lilacinus* on the pathogenesis of *Meloidogyne javanica* and tomato plant growth. *Iran Agric. Res.* 24, 67–76.
- Faizal Azizi, M. M., and Lau, H. Y. (2022). Advanced diagnostic approaches developed for the global menace of rice diseases: a review. *Can. J. Plant Pathol.* 1–25, 1–25. doi: 10.1080/07060661.2022.2053588
- Fan, D., Subramanian, S., and Smith, D. L. (2020). Plant endophytes promote growth and alleviate salt stress in *Arabidopsis thaliana*. *Sci. Rep.* 10:12740. doi: 10.1038/s41598-020-69713-5
- Farhat, H., Urooj, F., Shafique, H. A., Sultana, V., and Ehteshamul-Haque, S. (2017). Rhizobia suppress the root knot nematode and root rotting fungi on mungbean. *Int. J. Biol. Res.* 5, 71–75.
- Ferro, H. M., Souza, R., Lelis, F., Vieira, M., Silva, J. C. P. D., and Medeiros, F. H. V. D. (2020). Bacteria for cotton plant protection: disease control, crop yield and fiber quality. *Rev. Caatinga* 33, 43–53. doi: 10.1590/1983-21252020v33n105rc
- Fones, H. N., Bebbler, D. P., Chaloner, T. M., Kay, W. T., Steinberg, G., Gurr, S. J., et al. (2020). Threats to global food security from emerging fungal and oomycete crop pathogens. *Nat. Food* 1, 332–342. doi:10.1038/s43016-020-0075-0
- Fu, B., Olawole, O., and Beattie, G. A. (2021). Biological control and microbial ecology draft genome sequence data of *Glutamicibacter* sp. FBE-19, a bacterium antagonistic to the plant pathogen *Erwinia tracheiphila*. *Phytopathology* 111, 765–768. doi: 10.1094/PHYTO-09-20-0380-A
- Galloway, J. N., Townsend, A. R., Erisman, J. W., Bekunda, M., Cai, Z., Freney, J. R., et al. (2008). Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science* 320, 889–892. doi: 10.1126/science.1136674
- Gamalero, E., Lingua, G., Capri, F. G., Fusconi, A., Berta, G., and Lemanceau, P. (2004). Colonization pattern of primary tomato roots by *Pseudomonas fluorescens* A6RI characterized by dilution plating, flow cytometry, fluorescence, confocal and scanning electron microscopy. *FEMS Microbiol. Ecol.* 48, 79–87. doi: 10.1016/j.femsec.2003.12.012
- Gao, Q. -M., Zhu, S., Kachroo, P., and Kachroo, A. (2015). Signal regulators of systemic acquired resistance. *Front. Plant Sci.* 6:228. doi: 10.3389/fpls.2015.00228
- Gaziea-Soliman, M., Ameen, H. H., and El-kelany, U. S. (2017). Effect of treatment time on biocontrol efficacy of *Bacillus amyloliquefaciens*, *Lysinibacillus sphaericus* and their Fusants against root-knot nematode *Meloidogyne incognita* infecting tomato plants. *Middle East J. Agric. Res.* 6, 369–375.
- Ghazanfar, M. U., Hussan, M., Hamid, M. I., and Ansari, S. U. (2016). Utilization of biological control agents for the management of postharvest pathogens of tomato. *Pak. J. Bot.* 48, 2093–2100.
- Gilden, R. C., Huffling, K., and Sattler, B. (2010). Pesticides and health risks. *J. Obstet. Gynecol. Neonatal Nurs.* 39, 103–110. doi: 10.1111/j.1552-6909.2009.01092.x
- Girlanda, M., Perotto, S., Mönne-Loccoz, Y., Bergero, R., Lazzari, A., Défago, G., et al. (2001). Impact of biocontrol *Pseudomonas fluorescens* CHA0 and a genetically modified derivative on the diversity of culturable fungi in the cucumber rhizosphere. *Appl. Environ. Microbiol.* 67, 1851–1864. doi: 10.1128/AEM.67.4.1851-1864.2001
- Giron, D., Frago, E., Glevarec, G., Pieterse, C. M., and Dicke, M. (2013). Cytokinin as key regulators in plant–microbe–insect interactions: connecting plant growth and defence. *Funct. Ecol.* 27, 599–609. doi: 10.1111/1365-2435.12042
- Glare, T., Caradus, J., Gelernter, W., Jackson, T., Keyhani, N., Kohl, J., et al. (2012). Have biopesticides come of age? *Trends Biotechnol.* 30, 250–258. doi: 10.1016/j.tibtech.2012.01.003T
- Glick, B. (1995). The enhancement of plant growth by free-living bacteria. *Can. J. Microbiol.* 41, 109–117. doi: 10.1139/m95-015
- Glick, B. R. (2012). Plant growth-promoting bacteria: mechanisms and applications. *Scientifica* 2012:963401. doi: 10.6064/2012/963401
- Goh, C. H., Veliz Vallejos, D. F., Nicotra, A. B., and Mathesius, U. (2013). The impact of beneficial plant-associated microbes on plant phenotypic plasticity. *J. Chem. Ecol.* 39, 826–839. doi: 10.1007/s10886-013-0326-8
- Goswami, M., and Deka, S. (2020). Plant growth-promoting rhizobacteria—alleviators of abiotic stresses in soil: a review. *Pedosphere* 30, 40–61. doi: 10.1016/S1002-0160(19)60839-8
- Gouda, S., Kerry, R. G., Das, G., Paramithiotis, S., Shin, H. -S., and Patra, J. K. (2018). Revitalization of plant growth promoting rhizobacteria for sustainable development in agriculture. *Microbiol. Res.* 206, 131–140. doi: 10.1016/j.micres.2017.08.016
- Gowtham, H. G., Hariprasad, P., Nayak, S. C., and Niranjana, S. R. (2016). Application of rhizobacteria antagonistic to *Fusarium oxysporum* f. sp. *lycopersici*

- for the management of *Fusarium* wilt in tomato. *Rhizosphere* 2, 72–74. doi: 10.1016/j.rhisph.2016.07.008
- Gupta, G., Parihar, S. S., Ahirwar, N. K., Snehi, S. K., and Singh, V. (2015). Plant growth promoting rhizobacteria (PGPR): current and future prospects for development of sustainable agriculture. *J. Microb. Biochem. Technol.* 7, 096–102. doi: 10.4172/1948-5948.1000188
- Haas, D., and Keel, C. (2003). Regulation of antibiotic production in root colonizing *Pseudomonas* spp. and relevance for biological control of plant disease. *Annu. Rev. Phytopathol.* 41, 117–153. doi: 10.1146/annurev.phyto.41.052002.095656
- Habiba, N. R., Ali, S. A., Sultana, V., Ara, J., and Ehteshamul-Haque, S. (2016). Evaluation of biocontrol potential of epiphytic fluorescent *Pseudomonas* associated with healthy fruits and vegetables against root rot and root knot pathogens of mungbean. *Pak. J. Bot.* 48, 1299–1303.
- Hajek, A. E., Hurley, B. P., Kenis, M., Garnas, J. R., Bush, S. J., Wingfield, J. M. J., et al. (2016). Exotic biological control agents: a solution or contribution to arthropod invasions? *Biol. Invasions* 18, 953–969. doi: 10.1007/s10530-016-1075-8
- Hanawi, M. J. (2016). *Tagetes erecta* with native isolates of *Paecilomyces lilacinus* and *Trichoderma hamatum* in controlling root-knot nematode *Meloidogyne javanica* on tomato. *Int. J. Appl. Innov. Eng. Manag.* 5, 81–88.
- Harman, G. E., Howell, C. R., Viterbo, A., Chet, I., and Lorito, M. (2004). *Trichoderma* species—opportunistic, avirulent plant symbionts. *Nat. Rev. Microbiol.* 2, 43–56. doi: 10.1038/nrmicro797
- Heimpel, G. E., Yang, Y., Hill, J. D., and Ragsdale, D. W. (2013). Environmental consequences of invasive species: greenhouse gas emissions of insecticide use and the role of biological control in reducing emissions. *PLoS One* 8:e72293. doi: 10.1371/journal.pone.0072293
- Hernandez-Leon, R., Rojas-Solis, D., Contreras-Perez, M., Orozco-Mosqueda, M. C., Macias-Rodriguez, L. I., la Cruz, H. R. D., et al. (2015). Characterization of the antifungal and plant growth-promoting effects of diffusible and volatile organic compounds produced by *Pseudomonas fluorescens* strains. *Biol. Control* 81, 83–92. doi: 10.1016/j.biocontrol.2014.11.011
- Herridge, D. F., Peoples, M. B., and Boddey, R. M. (2008). Global inputs of biological nitrogen fixation in agricultural systems. *Plant Soil* 311, 1–18. doi: 10.1007/s11104-008-9668-3
- Hidayah, B. N., Khangura, R., and Dell, B. (2022). Biological control potential of *Trichoderma* species and bacterial antagonists against *Sclerotinia sclerotiorum* on canola in Western Australia. *Int. J. Agric. Biol.* 27, 215–227. doi: 10.17957/ijab/15.1919
- Hong, Y. W., Glick, B. R., and Pasternak, J. J. (1991). Plant microbial interaction under gnotobiotic conditions: a scanning electron microscope study. *Curr. Microbiol.* 23, 111–114. doi: 10.1007/bf02092259
- Hussain, M., Zouhar, M., and Ryšánek, P. (2017). Comparison between biological and chemical management of root-knot nematode, *Meloidogyne hapla*. *Pak. J. Zool.* 49, 205–210. doi: 10.17582/journal.pjz/2017.49.1.215.220
- Ibiang, S. R., Usami, T., and Sakamoto, K. (2021). Reduction of *Verticillium* wilt in tomato by an arbuscular mycorrhizal fungus-*Rhizophagus intraradices* and an endophytic fungus-*Penicillium piniophilum* is cultivar dependent. *Rhizosphere* 20:100440. doi: 10.1016/j.rhisph.2021.100440
- Inui Kishi, R. N., Galdiano Júnior, R. F., Val-Moraes, S. P., and Kishi, L. T. (2017). “Soil microbiome and their effects on nutrient management for plants,” in *Probiotics in Agroecosystem*. eds. V. Kumar, M. Kumar, S. Sharma and R. Prasad (Singapore: Springer), 117–143.
- Islam, S., Akanda, A. M., Prova, A., Islam, M. T., and Hossain, M. M. (2016). Isolation and identification of plant growth promoting rhizobacteria from cucumber rhizosphere and their effect on plant growth promotion and disease suppression. *Front. Microbiol.* 6:1360. doi: 10.3389/fmicb.2015.01360
- Jha, C. K., and Saraf, M. (2015). Plant growth promoting rhizobacteria (PGPR): a review. *E3 J. Agric. Res. Dev.* 2, 108–119. doi: 10.13140/RG.2.1.5171.2164
- Jha, S. N., Vishwakarma, R. K., Ahmad, T., Rai, A., and Dixit, A. K. (2015). *Technical report on assessment of quantitative harvest and post-harvest losses of major crops and commodities in India*. Ludhiana: ICAR All India Coordinated Research Project on Post-Harvest Technology, ICAR-CIPHET. doi: 10.13140/rg.2.1.3024.3924
- Jisha, M. S., Linu, M. S., and Sreekumar, J. (2018). Induction of systemic resistance in chilli (*Capsicum annuum* L.) by *Pseudomonas aeruginosa* against anthracnose pathogen *Colletotrichum capsici*. *J. Trop. Agric.* 56, 153–166.
- Jochum, M. D., McWilliams, K. L., Borrego, E. J., Kolomiets, M. V., Niu, G., Pierson, E. A., et al. (2019). Bioprospecting plant growth-promoting rhizobacteria that mitigate drought stress in grasses. *Front. Microbiol.* 10:2106. doi: 10.3389/fmicb.2019.02106
- Jones, E. E., Rabeendran, N., and Stewart, A. (2014). Biocontrol of *Sclerotinia sclerotiorum* infection of cabbage by *Coniothyrium minitans* and *Trichoderma* spp. *Biocontrol Sci. Tech.* 24, 1363–1382. doi: 10.1080/09583157.2014.940847
- Kakembo, D., and Lee, Y. H. (2019). Analysis of traits for biocontrol performance of *Pseudomonas parafulva* JBCS1880 against bacterial pustule in soybean plants. *Biol. Control* 134, 72–81. doi: 10.1016/j.biocontrol.2019.04.006
- Kalele, D. N., Affokpon, A., Coosemans, J., and Kimenju, J. (2010). Suppression of root-knot nematodes in tomato and cucumber using biological control agents. *Afr. J. Horticultural Sci.* 3, 72–80.
- Kamil, F. H., Saeed, E. E., El-Tarabily, K. A., and AbuQamar, S. F. (2018). Biological control of mango dieback disease caused by *Lasiodiplodia theobromae* using streptomycete and non-streptomycete actinobacteria in the United Arab Emirates. *Front. Microbiol.* 9:829. doi: 10.3389/fmicb.2018.00829
- Kang, S. M., Joo, G. J., Hamayun, M., Na, C. I., Shin, D. H., Kim, H. Y., et al. (2009). Gibberellin production and phosphate solubilization by newly isolated strain of *Acinetobacter calcoaceticus* and its effect on plant growth. *Biotechnol. Lett.* 31, 277–281. doi: 10.1007/s10529-008-9867-2
- Kang, S. W., Rahman, M. S., Kim, A. N., Lee, K. Y., Park, C. Y., Kerr, W. L., et al. (2017). Comparative study of the quality characteristics of defatted soy flour treated by supercritical carbon dioxide and organic solvent. *J. Food Sci. Technol.* 54, 2485–2493. doi: 10.1007/s13197-017-2691-8
- Kavitha, P. G., Jonathan, E. L., and Sankari Meena, K. (2013). Induction of defence enzymes in tomato by plant growth promoting rhizobacteria, *Pseudomonas fluorescens* against root-knot nematode, *Meloidogyne incognita*. *Indian J. Nematol.* 43, 94–96.
- Kazan, K., and Manners, J. M. (2009). Linking development to defense: auxin in plant–pathogen interactions. *Trends Plant Sci.* 14, 373–382. doi: 10.1016/j.tplants.2009.04.005
- Kerry, B. R., and Hidalgo-Diaz, L. (2004). Application of *Pochonia chlamydosporia* in the integrated control of root-knot nematodes on organically grown vegetable crops in Cuba. *Bull. IOBC/WPRS/SROP* 27, 123–126.
- Khafagi, E. Y., El-Syed, A., and Elwan, S. E. (2020). Controlling cabbage *Fusarium* wilt (yellows) using topsin M and some commercial biofertilizer products. *Zagazig J. Agric. Res.* 47, 519–530. doi: 10.21608/zjar.2020.94492
- Khalili, E., Sadravi, M., Naeimi, S., and Khorsavi, V. (2012). Biological control of rice brown spot with native isolates of three *Trichoderma* species. *Braz. J. Microbiol.* 43, 297–305. doi: 10.1590/S1517-838220120001000035
- Khan, A., Shaikat, S. S., Islam, S., and Khan, A. (2012). Evaluation of fluorescent *Pseudomonas* isolates for their activity against some plant-parasitic nematodes. *Am. Eurasian J. Agric. Environ. Sci.* 12, 1496–1506. doi: 10.5829/idosi.ajeas.2012.12.11.1841
- Khan, A., Tariq, M., Asif, M., Khan, F., Ansari, T., and Siddiqui, M. A. (2019). Integrated management of *Meloidogyne incognita* infecting *Vigna radiata* L. using biocontrol agent *Purpureocillium lilacinum*. *Trends Appl. Sci. Res.* 14, 119–124. doi: 10.3923/tasr.2019.119.124
- Khatun, A., Farhana, T., Sabir, A. A., Islam, S., West, H. M., Rahman, M., et al. (2018). *Pseudomonas* and *Burkholderia* inhibit growth and asexual development of *Phytophthora capsici*. *Z. Naturforsch. C J. Biosci.* 73, 123–135. doi: 10.1515/znc-2017-0065
- Kim, Y. S., Song, J. G., Lee, I. K., Yeo, W. H., and Yun, B. S. (2013). *Bacillus* sp. BS061 suppresses powdery mildew and gray mold. *Mycobiology* 41, 108–111. doi: 10.5941/myco.2013.41.2.108
- Kiriga, A. W., Haukeland, S., Kariuki, G. M., Coyne, D. L., and Beek, N. V. (2018). Effect of *Trichoderma* spp. and *Purpureocillium lilacinum* on *Meloidogyne javanica* in commercial pineapple production in Kenya. *Biol. Control* 119, 27–32. doi: 10.1016/j.biocontrol.2018.01.005
- Kiss, L. (2003). A review of fungal antagonists of powdery mildews and their potential as biocontrol agents. *Pest Manag. Sci.* 59, 475–483. doi: 10.1002/ps.689
- Kloepper, J. W., Leong, J., Teintze, M., and Schroth, M. N. (1980). Enhanced plant growth by siderophores produced by plant growth-promoting rhizobacteria. *Nature* 286, 885–886. doi: 10.1038/286885a0
- Köhl, J., Kolnaar, R., and Ravensberg, W. J. (2019). Mode of action of microbial biological control agents against plant diseases: relevance beyond efficacy. *Front. Plant Sci.* 10:845. doi: 10.3389/fpls.2019.00845
- Kumar, S., Chauhan, P. S., Agrawal, L., Raj, R., Srivastava, A., Gupta, S., et al. (2016). *Paenibacillus lentimorbus* inoculation enhances tobacco growth and attenuates the virulence of cucumber mosaic virus. *PLoS One* 11:e0149980. doi: 10.1371/journal.pone.0149980
- Kumar, V., Singh, A. U., and Jain, R. K. (2012). Comparative efficacy of bioagents as seed treatment for management of *Meloidogyne incognita* infecting okra. *Nematologia Mediterr.* 40, 209–211.
- Lamont, J. R., Wilkins, O., Bywater-Ekegard, M., and Smith, D. L. (2017). From yogurt to yield: potential applications of lactic acid bacteria in plant production. *Soil Biol. Biochem.* 111, 1–9. doi: 10.1016/j.soilbio.2017.03.015
- Lee, Y. S., and Kim, K. Y. (2016). Antagonistic potential of *Bacillus pumilus* L1 against root-knot nematode, *Meloidogyne arenaria*. *J. Phytopathol.* 164, 29–39. doi: 10.1111/jph.12421
- Lee, S. K., Lur, H. S., Lo, K. J., Cheng, K. C., Chuang, C. C., Tang, S. J., et al. (2016). Evaluation of the effects of different liquid inoculant formulations on the survival and plant-growth-promoting efficiency of *Rhodospseudomonas palustris* strain PS3. *Appl. Microbiol. Biotechnol.* 100, 7977–7987. doi: 10.1007/s00253-016-7582-9

- Leontidou, K., Genitsaris, S., Papadopoulou, A., Kamou, N., Bosmali, I., Matsi, T., et al. (2020). Plant growth promoting rhizobacteria isolated from halophytes and drought-tolerant plants: genomic characterization and exploration of phyto-beneficial traits. *Sci. Rep.* 10:14857. doi: 10.1038/s41598-020-71652-0
- Li, Y., Feng, X., Wang, X., Zheng, L., and Liu, H. (2020). Inhibitory effects of *Bacillus licheniformis* BL06 on *Phytophthora capsici* in pepper by multiple modes of action. *Biol. Control* 144:104210. doi: 10.1016/j.biocontrol.2020.104210
- Li, G. H., Zhang, K. Q., Xu, J. P., Dong, J. Y., and Liu, Y. J. (2007). Nematicidal substances from fungi. *Recent Pat. Biotechnol.* 1, 212–233. doi: 10.2174/187220807782330165
- Liu, X., Bimerew, M., Ma, Y., Muller, H., Ovadis, M., Eberl, L., et al. (2007). Quorum sensing signaling is required for production of the antibiotic pyrrolnitrin in a rhizospheric biocontrol strain of *Serratia plymuthica*. *FEMS Microbiol. Lett.* 270, 299–305. doi: 10.1111/j.1574-6968.2007.00681.x
- Liu, Y., Chen, Z., Liu, L., Han, P., Wang, X., Li, S., et al. (2022). Broad-spectrum antifungal activity of lipopeptide brevilaterin B and its inhibition effects against *Fusarium oxysporum* and *Penicillium chrysogenum*. *J. Appl. Microbiol.* 132, 1330–1342. doi: 10.1111/jam.15285
- Liu, K., McInroy, J. A., Hu, C. H., and Kloepper, J. W. (2018). Mixtures of plant-growth-promoting rhizobacteria enhance biological control of multiple plant diseases and plant-growth promotion in the presence of pathogens. *Plant Dis.* 102, 67–72. doi: 10.1094/pdis-04-17-0478-re
- Llorente, B. E., Alasia, M. A., and Larraburu, E. E. (2016). Biofertilization with *Azospirillum brasilense* improves *in vitro* culture of *Handroanthus ochraceus*, a forestry, ornamental and medicinal plant. *N. Biotechnol.* 33, 32–40. doi: 10.1016/j.nbt.2015.07.006
- Lobo, C. B., Juárez Tomás, M. S., Viruel, E., Ferrero, M. A., and Lucca, M. E. (2019). Development of low-cost formulations of plant growth-promoting bacteria to be used as inoculants in beneficial agricultural technologies. *Microbiol. Res.* 219, 12–25. doi: 10.1016/j.micres.2018.10.012
- Lommen, S. T. E., Koops, K. G., Cornelder, B. A., de Jong, P. W., and Brakefield, P. M. (2019). Genetics and selective breeding of variation in wing truncation in a flightless aphid control agent. *Entomol. Exp. Appl.* 167, 636–645. doi: 10.1111/eea.12810
- Lucas, J. (2011). Advance in plant disease and pest management. *J. Agric. Sci.* 149, 91–114. doi: 10.1017/S0021859610000997
- Lugtenberg, B., and Kamilova, F. (2009). Plant growth promoting rhizobacteria. *Annu. Rev. Microbiol.* 63, 541–556. doi: 10.1146/annurev.micro.62.081307.162918
- Lyu, D., Backer, R., Subramanian, S., and Smith, D. (2020). Phytomicrobiome coordination signals hold potential for climate change-resilient agriculture. *Front. Plant Sci.* 11:634. doi: 10.3389/fpls.2020.00634
- Maksimov, I. V., Abizgildina, R. R., and Pusenkova, L. I. (2011). Plant growth promoting rhizobacteria as alternative to chemical crop protectors from pathogens (review). *Appl. Biochem. Microbiol.* 47, 333–345. doi: 10.1134/S0003683811040090
- Maksimov, I. V., Blagova, D. K., Veselova, S. V., Sorokan, A. V., Burkhanova, G. F., and Cherepanova, E. A. (2020). Recombinant *Bacillus subtilis* 26DCryChS line with gene Bcry11a encoding Cry11a toxin from *Bacillus thuringiensis* promotes integrated wheat defense against pathogen *Stagonospora nodorum* Berk and greenbug *Schizaphis graminum* Rond. *Biol. Control* 144:104242. doi: 10.1016/j.biocontrol.2020.104242
- Mathys, J., De Cremer, K., Timmermans, P., Van Kerckhove, S., Lievens, B., Vanhaecke, M., et al. (2012). Genome-wide characterization of ISR induced in *Arabidopsis thaliana* by *Trichoderma hamatum* T382 against *Botrytis cinerea* infection. *Front. Plant Sci.* 3:108. doi: 10.3389/fpls.2012.00108
- Mau, Y. S., Prayetno, R. S., Kaka, H., Naat, K. D., Henuk, J. B. D., Hahuly, M. V., et al. (2022). Efficacy of indigenous *Trichoderma* isolates of West Timor, Indonesia, as biocontrol agents of brown spot (*Drechslera oryzae*) on two upland rice varieties. *Egypt J. Biol. Pest Control* 32, 1–10. doi: 10.1186/s41938-022-00559-x
- Mauch-Mani, B., Baccelli, I., Luna, E., and Flors, V. (2017). Defense priming: an adaptive part of induced resistance. *Annu. Rev. Plant Biol.* 68, 485–512. doi: 10.1146/annurev-arplant-042916-041132
- Maung, C. E. H., Baek, W. S., Choi, T. G., and Kim, K. Y. (2021). Control of grey mould disease on strawberry using the effective agent, *Bacillus amyloliquefaciens* Y1. *Biocontrol Sci. Technol.* 31, 468–482. doi: 10.1080/09583157.2020.1867707
- McIntyre, J. L., and Press, L. S. (1991). "Formulation, delivery systems and marketing of biocontrol agents and plant growth promoting rhizobacteria (PGPR)," in *The Rhizosphere and plant growth. Beltsville symposia in agricultural research*. eds. D. L. Keister and P. B. Cregan (Dordrecht: Springer), 289–295.
- Mengiste, T., Laluk, K., and AbuQamar, S. (2010). "Mechanisms of induced resistance against *B. cinerea*," in *Post-Harvest Pathology, Plant Pathology in the 21st Century*. vol. 2 eds. D. Prusky and M. L. Gullino, (Dordrecht: Springer), 13–30.
- Mishra, J., Tewari, S., Singh, S., and Arora, N. (2015). "Biopesticides: where we stand?" in *Plant Microbes Symbiosis: Applied Facets*. ed. N. Arora (New Delhi: Springer), 37–75. doi: 10.1007/978-81-322-2068-8_2
- Mohammadi, P., Tozlu, E., Kotan, R., and Kotan, M. S. (2017). Potential of some bacteria for biological control of postharvest citrus green mold caused by *Penicillium digitatum*. *Plant Prot. Sci.* 53, 134–143. doi: 10.17221/55/2016-PPS
- Mohan, L. K., Kurein, S., and Sreeja, P. (2017). Management of *Meloidogyne incognita* in *Solenostemon rotundifolius* (Poir) Morton. *Indian J. Nematol.* 47, 1–5.
- Muller, H., and Berg, G. (2008). Impact of formulation procedures on the effect of the biocontrol agent *Serratia plymuthica* HROC48 on *Verticillium* wilt in oilseed rape. *BioControl* 53, 905–916. doi: 10.1007/s10526-007-9111-3
- Müller, K., Kramer, S., Haslwimmer, H., Marhan, S., Scheunemann, N., Butenschön, O., et al. (2016). Carbon transfer from maize roots and litter into bacteria and fungi depends on soil depth and time. *Soil Biol. Biochem.* 93, 79–89. doi: 10.1016/j.soilbio.2015.10.015
- Murugan, L., Krishnan, N., Venkataravanappa, V., Saha, S., Mishra, A. K., Sharma, B. K., et al. (2020). Molecular characterization and race identification of *Fusarium oxysporum* f. sp. *lycopersici* infecting tomato in India. *3 Biotech* 10, 1–12. doi: 10.1007/s13205-020-02475-z
- Musilova, L., Ridl, J., Polivkova, M., Macek, T., and Uhlik, O. (2016). Effects of secondary plant metabolites on microbial populations: changes in community structure and metabolic activity in contaminated environments. *Int. J. Mol. Sci.* 17:1205. doi: 10.3390/ijms17081205
- Nabila, N., and Kasiamdari, R. S. (2021). Antagonistic activity of siderophore-producing bacteria from black rice rhizosphere against rice blast fungus *Pyricularia oryzae*. *Microbiol. Biotechnol. Lett.* 49, 217–224. doi: 10.48022/mb.2011.11009
- Nakashita, H., Yasuda, M., Nitta, T., Asami, T., Fujioka, S., Arai, Y., et al. (2003). Brassinosteroid functions in a broad range of disease resistance in tobacco and rice. *Plant J.* 33, 887–898. doi: 10.1046/j.1365-3113x.2003.01675.x
- Nally, M. C., Pesce, V. M., Maturano, Y. P., Muñoz, C. J., Combina, M., Toro, M. E., et al. (2012). Biocontrol of *Botrytis cinerea* in table grapes by non-pathogenic indigenous *Saccharomyces cerevisiae* yeasts isolated from viticultural environments in Argentina. *Postharvest Biol. Technol.* 64, 40–48. doi: 10.1016/j.postharvbio.2011.09.009
- Nasima, I. A., Imran, A. S., Shahid, S. S., and Zaki, M. J. (2002). Nematicidal activity of some strains of *Pseudomonas* spp. *Soil Biol. Biochem.* 34, 1051–1058. doi: 10.1016/s0038-0717(02)00029-9
- Nazari, M., and Smith, D. L. (2020). A PGPR-produced bacteriocin for sustainable agriculture: a review of thuricin 17 characteristics and applications. *Front. Plant Sci.* 11:916. doi: 10.3389/fpls.2020.00916
- Nielsen, T. H., Sorensen, D., Tobiasen, C., Andersen, J. B., Christophersen, C., Givskov, M., et al. (2002). Antibiotic and biosurfactant properties of cyclic lipopeptides produced by fluorescent *Pseudomonas* spp. from the sugar beet rhizosphere. *Appl. Environ. Microbiol.* 68, 3416–3423. doi: 10.1128/AEM.68.7.3416-3423.2002
- Nivedhitha, V. R., Shweta, B., Deepa, D. D., Manojkumar, N. H., and Raghavendra, R. B. (2008). Plant growth promoting microorganisms (PGPMs) from bamboo rhizosphere. *J. Adv. Biotechnol.* 7, 33–35.
- Nunes, C. A. (2012). Biological control of postharvest diseases of fruit. *Eur. J. Plant Pathol.* 133, 181–196. doi: 10.1007/s10658-011-9919-7
- O'Brien, P. A. (2017). Biological control of plant diseases. *Australas. Plant Pathol.* 46, 293–304. doi: 10.1007/s13313-017-0481-4
- Ongena, M., and Jacques, P. (2008). *Bacillus* lipopeptides: versatile weapons for plant disease biocontrol. *Trends Microbiol.* 16, 115–125. doi: 10.1016/j.tim.2007.12.009
- Pal, K. K., and Gardener, B. M. (2006). Biological control of plant pathogens. *Plant Health Instr.*, 1–25. doi: 10.1094/PHI-A-2006-1117-02
- Park, K., Park, J. W., Lee, S. W., and Balaraju, K. (2013). Induced suppression of soft rot disease in tobacco by combined application of *Bacillus subtilis* strain B4 and chemical elicitor BTH. *Biocontrol Sci. Tech.* 23, 968–979. doi: 10.1080/09583157.2013.811467
- Parveen, G., Noreen, R., Shafique, H. A., Sultana, V., Ehteshamul-Haque, S., and Athar, M. (2019). Role of rhizobia in suppressing the root diseases of soybean under soil amendment. *Planta Daninha* 37:e019172336. doi: 10.1590/s0100-83582019370100038
- Patkowska, E. (2021). Biostimulants managed fungal phytopathogens and enhanced activity of beneficial microorganisms in rhizosphere of *Scorzonera* (*Scorzonera hispanica* L.). *Agriculture* 11:347. doi: 10.3390/agriculture11040347
- Pendse, M. A., Karwande, P. P., and Limaye, M. N. (2013). Past, present and future of nematophagous fungi as bio-agent to control plant parasitic nematodes. *J. Plant Prot. Sci.* 5, 1–9.
- Peng, D., Li, S., Wang, J., Chen, C., and Zhou, M. (2014). Integrated biological and chemical control of rice sheath blight by *Bacillus subtilis* NJ-18 and jinggangmycin. *Pest Manag. Sci.* 70, 258–263. doi: 10.1002/ps.3551
- Pérez-de-Luque, A., Tille, S., Johnson, I., Pascual-Pardo, D., Ton, J., and Cameron, D. D. (2017). The interactive effects of arbuscular mycorrhiza and plant

- growth-promoting rhizobacteria synergistically enhance host plant defences against pathogens. *Sci. Rep.* 7:16409. doi: 10.1038/s41598-017-16697-4
- Pieterse, C. M., Zamioudis, C., Does, D. V., and Van Wees, S. (2014). "Signalling networks involved in induced resistance," in *Induced Resistance for Plant Defense: A Sustainable Approach to Crop Protection*. eds. D. R. Walters, A. C. Newton, and G. D. Lyon (New York: John Wiley and Sons), 58–80.
- Pii, Y., Mimmo, T., Tomasi, N., Terzano, R., Cesco, S., and Crecchio, C. (2015). Microbial interactions in the rhizosphere: beneficial influences of plant growth promoting rhizobacteria on nutrient acquisition process. A review. *Biol. Fertil. Soils* 51, 403–415. doi: 10.1007/s00374-015-0996-1
- Prince, L., Raja, A., and Prabakaran, P. (2011). Antagonistic potentiality of some soil mycoflora against *Colletotrichum falcatum*. *World J. Sci. Technol.* 1, 39–42.
- Priya, M. S., and Kumar, S. (2006). Dose optimization of *Paecilomyces lilacinus* for the control of *Meloidogyne incognita* on tomato. *Indian J. Nematol.* 36, 27–31.
- Punja, Z. K., Rodriguez, G., and Tirajoh, A. (2016). Effects of *Bacillus subtilis* strain QST 713 and storage temperatures on post-harvest disease development on greenhouse tomatoes. *Crop Prot.* 84, 98–104. doi: 10.1016/j.cropro.2016.02.011
- Punja, Z. K., and Utkhede, R. S. (2003). Using fungi and yeasts to manage vegetable crop diseases. *Trends Biotechnol.* 21, 400–407. doi: 10.1016/S0167-7799(03)00193-8
- Qiao, J., Yu, X., Liang, X., Liu, Y., Borriss, R., and Liu, Y. (2017). Addition of plant-growth-promoting *Bacillus subtilis* PTS-394 on tomato rhizosphere has no durable impact on composition of root microbiome. *BMC Microbiol.* 17:131. doi: 10.1186/s12866-017-1039-x
- Raaijmakers, J. M., and Mazzola, M. (2012). Diversity and natural functions of antibiotics produced by beneficial and plant pathogenic bacteria. *Annu. Rev. Phytopathol.* 50, 403–424. doi: 10.1146/annurev-phyto-081211-172908
- Raaijmakers, J. M., Vlami, M., and de Souza, J. T. (2002). Antibiotic production by bacterial biocontrol agents. *Antonie Van Leeuwenhoek* 81, 537–547. doi: 10.1023/A:1020501420831
- Rady, M. M., Boriak, S. H. K., Abd El-Mageed, T. A., Seif El-Yazal, M. A., Ali, E. F., Hassan, F. A. S., et al. (2021). Exogenous gibberellic acid or dilute bee honey boosts drought stress tolerance in *Vicia faba* by rebalancing osmoprotectants, antioxidants, nutrients, and phytohormones. *Plants* 10:748. doi: 10.3390/plants10040748
- Radzki, W., Gutierrez Mañero, F., Algar, E., Lucas, J., García, J. A., García-Villaraco, A., et al. (2013). Bacterial siderophores efficiently provide iron to iron-starved tomato plants in hydroponics culture. *Antonie Van Leeuwenhoek* 104, 321–330. doi: 10.1007/s10482-013-9954-9
- Rahman, A., Korejo, F., Sultana, V., Ara, J., and Ehteshamulhaque, S. (2017). Induction of systemic resistance in cotton by the plant growth promoting rhizobacterium and seaweed against charcoal rot disease. *Pak. J. Bot.* 49, 347–353.
- Rao, M. S. (2007). Biopesticides for the management of nematodes in horticultural crops. *Indian J. Plant Prot.* 35, 202–205.
- Raza, W., Ling, N., Yang, L., Huang, Q., and Shen, Q. (2016). Response of tomato wilt pathogen *Ralstonia solanacearum* to the volatile organic compounds produced by a biocontrol strain *Bacillus amyloliquefaciens* SQR-9. *Sci. Rep.* 6:24856. doi: 10.1038/srep24856
- Rivera-Méndez, W., Obregón, M., Morán-Diezb, M. E., Hermosab, R., and Monteb, E. (2020). *Trichoderma asperellum* biocontrol activity and induction of systemic defenses against *Sclerotium cepivorum* in onion plants under tropical climate conditions. *Biol. Control* 141:104145. doi: 10.1016/j.biocontrol.2019.104145
- Rosier, A., Medeiros, F. H. V., and Bais, H. P. (2018). Defining plant growth promoting rhizobacteria molecular and biochemical networks in beneficial plant-microbe interactions. *Plant Soil* 428, 35–55. doi: 10.1007/s11104-018-3679-5
- Ruzzi, M., and Aroca, R. (2015). Plant growth-promoting rhizobacteria act as biostimulants in horticulture. *Sci. Hort.* 196, 124–134. doi: 10.1016/j.scienta.2015.08.042
- Saeed, E. E., Sham, A., Salmin, Z., Abdelmowla, Y., Iratni, R., El-Tarabily, K., et al. (2017). *Streptomyces globosus* UAE1, a potential effective biocontrol agent for black scorch disease in date palm plantations. *Front. Microbiol.* 8:1455. doi: 10.3389/fmicb.2017.01455
- Salomon, M. V., Funes Pinter, I., Piccoli, P., and Bottini, R. (2017). "Use of plant growth-promoting rhizobacteria as biocontrol agents: induced systemic resistance against biotic stress in plants," in *Microbial Applications: Biomedicine, Agriculture and Industry*. ed. V. C. Kalia (Cham: Springer International Publishing), 133–152. doi: 10.1007/978-3-319-52669-0_7
- Sánchez-Montesinos, B., Mila Santos, M., Moreno-Gavira, A., Marín-Rodulfo, T., Gea, F. J., and Diáñez, F. (2021). Biological control of fungal diseases by *Trichoderma aggressivum* f. *europaeum* and its compatibility with fungicides. *J. Fungi* 7:598. doi: 10.3390/jof7080598
- Sanzani, S., Reverberi, M., and Geisen, R. (2016). Mycotoxins in harvested fruits and vegetables: insights in producing fungi, biological role, conducive conditions, and tools to manage postharvest contamination. *Postharvest Biol. Technol.* 122, 95–105. doi: 10.1016/j.postharvbio.2016.07.003
- Savary, S., Willocquet, L., Pethybridge, S. J., Esker, P., McRoberts, N., and Nelson, A. (2019). The global burden of pathogens and pests on major food crops. *Nat. Ecol. Evol.* 3, 430–439. doi: 10.1038/s41559-018-0793-y
- Savchuk, S., and Fernando, W. D. D. (2004). Effect of timing of application and population dynamics on the degree of biological control of *Sclerotinia sclerotiorum* by bacterial antagonists. *FEMS Microbiol. Ecol.* 49, 379–388. doi: 10.1016/j.femsec.2004.04.014
- Sham, A., Al-Ashram, H., Whitley, K., Iratni, R., El-Tarabily, K. A., and AbuQamar, S. F. (2019). Metatranscriptomic analysis of multiple environmental stresses identifies RAP2.4 gene associated with *Arabidopsis* immunity to *Botrytis cinerea*. *Sci. Rep.* 9:17010. doi: 10.1038/s41598-019-53694-1
- Sham, A., Moustafa, K., Al-Shamisi, S., Alyan, S., Iratni, R., and AbuQamar, S. F. (2017). Microarray analysis of *Arabidopsis* WRKY33 mutants in response to the necrotrophic fungus *Botrytis cinerea*. *PLoS One* 12:e0172343. doi: 10.1371/journal.pone.0172343
- Shanthiyaa, V., Karthikeyan, G., and Raguchander, T. (2013). Production of extracellular proteins, cellulases and antifungal metabolites by *Chaetomium globosum* Kunze ex. Fr. *Arch. Phytopathol. Plant Prot.* 47, 517–528. doi: 10.1080/03235408.2013.813124
- Sharf, R., Shiekh, H., Syed, A., Akhtar, A., and Robab, A. (2014). Interaction between *Meloidogyne incognita* and *Pochonia chlamydosporia* and their effects on the growth of *Phaseolus vulgaris*. *Arch. Phytopathol. Plant Prot.* 47, 622–630. doi: 10.1080/03235408.2013.816459
- Shen, X., Hu, H., Peng, H., Wang, W., and Zhang, X. (2013). Comparative genomic analysis of four representative plant growth-promoting rhizobacteria in *Pseudomonas*. *BMC Genomics* 14:271. doi: 10.1186/1471-2164-14-271
- Shivlata, L., and Satyanarayana, T. (2017). "Actinobacteria in agricultural and environmental sustainability," in *Agro-Eenvironmental Sustainability*. eds. J. S. Singh and G. Seneviratne (Berlin: Springer), 173–218.
- Siddiqui, I. A., and Shaikat, S. S. (2004). *Trichoderma harzianum* enhances the production of nematicidal compounds *in vitro* and improves biocontrol of *Meloidogyne javanica* by *Pseudomonas fluorescens* in tomato. *Lett. Appl. Microbiol.* 38, 169–175. doi: 10.1111/j.1472-765x.2003.01481.x
- Silva, S. D., Carneiro, R. M. D. G., Faria, M., Souza, D. A., Monnerat, R. G., and Lopes, R. B. (2017). Evaluation of *Pochonia chlamydosporia* and *Purpureocillium lilacinum* for suppression of *Meloidogyne enterolobii* on tomato and banana. *J. Nematol.* 49, 77–85. doi: 10.21307/jofnem-2017-047
- Singh, S., Prem, D., and Tanwar, R. S. (2005). Production and antifungal activity of secondary metabolites of *Trichoderma virens*. *Pestic. Res. J.* 17, 26–29.
- Singh, N., Singh, D., and Singh, N. (2017). Effect of *Glomus bagyaraji* inoculation and phosphorus amendments on *Fusarium* wilt of chickpea. *Agric. Res. J.* 54, 236–243. doi: 10.5958/2395-146X.2017.00043.6
- Sivasakthi, S., Usharani, G., and Saranraj, P. (2014). Biocontrol potentiality of plant growth promoting bacteria (PGPR)-*Pseudomonas fluorescens* and *Bacillus subtilis*. A review. *Afr. J. Agric. Res.* 9, 1265–1277. doi: 10.5897/AJAR
- Snehalatharani, A., Devappa, V., and Sangeetha, C. G. (2021). "Postharvest diseases of banana and their management," in *Postharvest Handling and Diseases of Horticultural Produce*. eds. D. Singh, R. R. Sharma, V. Devappa and D. Kamil (Boca Raton: CRC Press), 201–210.
- Spadaro, D., and Gullino, M. L. (2005). Improving the efficacy of biocontrol agents against soil borne pathogens. *Crop Prot.* 24, 601–613. doi: 10.1016/j.cropro.2004.11.003
- Spaepen, S., Bossuyt, S., Engelen, K., Marchal, K., and Vanderleyden, J. (2014). Phenotypic and molecular responses of *Arabidopsis thaliana* roots as a result of inoculation with the auxin-producing bacterium *Azospirillum brasilense*. *New Phytol.* 201, 850–861. doi: 10.1111/nph.12590
- Stirling, G. R. (2017). "Biological control of plant-parasitic nematodes," in *Diseases of Nematodes*. eds. G. O. Poinar and H. B. Jansson (Boca Raton: CRC Press), 103–150.
- Subramanian, S., and Smith, D. L. (2015). Bacteriocins from the rhizosphere microbiome: from an agriculture perspective. *Front. Plant Sci.* 6:909. doi: 10.3389/fpls.2015.00909
- Sui, Y., Wang, Z., Zhang, D., and Wang, Q. (2021). Oxidative stress adaptation of the antagonistic yeast, *Debaryomyces hansenii*, increases fitness in the microenvironment of kiwi fruit wound and biocontrol efficacy against postharvest diseases. *Biol. Control* 152:104428. doi: 10.1016/j.biocontrol.2020.104428
- Sultana, F., and Hossain, M. M. (2022). Assessing the potentials of bacterial antagonists for plant growth promotion, nutrient acquisition, and biological control of southern blight disease in tomato. *PLoS One* 17:e0267253. doi: 10.1371/journal.pone.0267253
- Takishita, Y., Charron, J. B., and Smith, D. L. (2018). Biocontrol rhizobacterium *Pseudomonas* sp. 23s induces systemic resistance in tomato (*Solanum lycopersicum* L.) against bacterial canker *Clavibacter michiganensis* subsp. *michiganensis*. *Front. Microbiol.* 9:2119. doi: 10.3389/fmicb.2018.02119

- Tariq, M., Khan, A., Asif, M., Khan, F., Ansari, T., Shariq, M., et al. (2020). Biological control: a sustainable and practical approach for plant disease management. *Acta Agric. Scand. B Soil Plant Sci.* 70, 507–524. doi: 10.1080/09064710.2020.1784262
- Tariq, M., Khan, A., Asif, M., and Siddiqui, M. A. (2018). Interactive effect of *Trichoderma virens* and *Meloidogyne incognita* and their influence on plant growth character and nematode multiplication on *Abelmoschus esculentus* (L.) Moench. *Current Nematol.* 29, 1–9.
- Timper, P. (2011). "Utilization of biological control for managing plant-parasitic nematodes," in *Biological Control of Plant-Parasitic Nematodes: Building Coherence Between Microbial Ecology and Molecular Mechanisms*. eds. K. Davies and S. Spiegel (Dordrecht: Springer), 259–289.
- Torres, M. J., Brandan, C. P., Petroselli, G., Erra-Balsells, R., and Audisio, M. C. (2016). Antagonistic effects of *Bacillus subtilis* subsp. *subtilis* and *B. amyloliquefaciens* against *Macrophomina phaseolina*: SEM study of fungal changes and UV-MALDI-TOF MS analysis of their bioactive compounds. *Microbiol. Res.* 182, 31–39. doi: 10.1016/j.micres.2015.09.005
- Tsegaye, Z., Assefa, F., Tefera, G., Alemu, T., Gizaw, B., and Abatenh, E. (2018). Concept, principle and application of biological control and their role in sustainable plant diseases management strategies. *Int. J. Res. Stud. Biosci.* 6, 18–34. doi: 10.20431/2349-0365.0604004
- Usman, A., and Siddiqui, M. A. (2012). Effect of some fungal strains for the management of root-knot nematode (*Meloidogyne incognita*) on eggplant (*Solanum melongena*). *J. Agric. Technol.* 8, 213–218.
- Vacheron, J., Desbrosses, G., Bouffaud, M. L., Touraine, B., MoenneLoccoz, Y., Muller, D., et al. (2013). Plant growth-promoting rhizobacteria and root system functioning. *Front. Plant Sci.* 4:356. doi: 10.3389/fpls.2013.00356
- Vejan, P., Abdullah, R., Khadiran, T., Ismail, S., and Nasrulhaq Boyce, A. (2016). Role of plant growth promoting rhizobacteria in agricultural sustainability: a review. *Molecules* 21:573. doi: 10.3390/molecules21050573
- Viaene, N., Coyne, D. L., and Kerry, B. R. (2006). "Biological and cultural management," in *Plant nematology*. eds. R. N. Perry and M. Moens (Wallingford: CAB), 346–369.
- Viejobueno, J., Albornoz, P. L., Camacho, M., de los Santos, B., Martínez-Zamora, M. G., and Salazar, S. M. (2021). Protection of strawberry plants against charcoal rot disease (*Macrophomina phaseolina*) induced by *Azospirillum brasilense*. *Agronomy* 11:195. doi: 10.3390/agronomy11020195
- Vinale, F., Flematti, G., Sivasithamparam, K., Lorito, M., Marra, R., Skelton, B. W., et al. (2009). Harzianic acid, an antifungal and plant growth promoting metabolite from *Trichoderma harzianum*. *J. Nat. Prod.* 72, 2032–2035. doi: 10.1021/np900548p
- Vitorino, L. C., Silva, F., Cruvinel, B. G., Bessa, L. A., Rosa, M., Souchie, E. L., et al. (2020). Biocontrol potential of *Sclerotinia sclerotiorum* and physiological changes in soybean in response to *Butia archeri* palm rhizobacteria. *Plan. Theory* 9:64. doi: 10.3390/plants9010064
- Vos, C. M., Tesfahun, A. N., Panis, B., De Waele, D., and Elsen, A. (2012). Arbuscular mycorrhizal fungi induce systemic resistance in tomato against the sedentary nematode *Meloidogyne incognita* and the migratory nematode *Pratylenchus penetrans*. *Appl. Soil Ecol.* 61, 1–6. doi: 10.1016/j.apsoil.2012.04.007
- Wallace, R. L., Hirkala, D. L., and Nelson, L. M. (2018). Efficacy of *Pseudomonas fluorescens* for control of *Mucor* rot of apple during commercial storage and potential modes of action. *Can. J. Microbiol.* 64, 420–431. doi: 10.1139/cjm-2017-0776
- Wang, M., Geng, L., Sun, X., Shu, C., Song, F., and Zhang, J. (2020). Screening of *Bacillus thuringiensis* strains to identify new potential biocontrol agents against *Sclerotinia sclerotiorum* and *Plutella xylostella* in *Brassica campestris* L. *Biol. Control* 145, 104262–104269. doi: 10.1016/j.biocontrol.2020.104262
- Watanabe, A., Kamei, K., Sekine, T., Waku, M., Nishimura, K., Miyaji, M., et al. (2004). Effect of aeration on gliotoxin production by *Aspergillus fumigatus* in its culture filtrate. *Mycopathologia* 157, 19–27. doi: 10.1023/b:myco.0000012224.49131.dd
- Weller, D. M. (2007). *Pseudomonas* biocontrol agents of soil borne pathogens: looking back over 30 years. *Phytopathology* 97, 250–256. doi: 10.1094/PHYTO-97-2-0250
- Whipps, J. M. (2001). Microbial interactions and biocontrol in the rhizosphere. *J. Exp. Bot.* 52, 487–511. doi: 10.1093/jxb/52.suppl_1.487
- Yao, X., Huang, K., Zhao, S., Cheng, Q., Zhang, S., Yang, L., et al. (2021). Identification and verification of rhizosphere indicator microorganisms in tobacco root rot. *Agron. J.* 113, 1480–1491. doi: 10.1002/agj2.20547
- Yones, A. M., and kayim, M. (2021). Molecular characterization of *Trichoderma* spp. with biocontrol ability against faba bean chocolate spot (*Botrytis cinerea* Pers. ex Fr.). *Plant Cell Biotechnol. Mol. Biol.* 22, 52–63.
- Zamioudis, C., and Pieterse, C. M. (2012). Modulation of host immunity by beneficial microbes. *Mol. Plant Microbe Interact.* 25, 139–150. doi: 10.1094/MPMI-06-11-0179
- Zapata-Sarmiento, D. H., Palacios-Pala, E. F., Rodríguez-Hernández, A. A., Melchor, D. L. M., Rodríguez-Monroy, M., and Sepúlveda-Jiménez, G. (2020). *Trichoderma asperellum*, a potential biological control agent of *Stemphylium vesicarium*, on onion (*Allium cepa* L.). *Biol. Control* 140:104105. doi: 10.1016/j.biocontrol.2019.104105
- Zgadaj, R., Garrido-Oter, R., Jensen, D. B., Koprivova, A., SchulzeLefert, P., and Radutoiu, S. (2016). Root nodule symbiosis in *Lotus japonicus* drives the establishment of distinctive rhizosphere, root, and nodule bacterial communities. *Proc. Natl. Acad. Sci. USA* 113, E7996–E8005. doi: 10.1073/pnas.1616564113
- Zhang, Y., Li, T., Xu, M., Guo, J., Zhang, C., Feng, Z., et al. (2021b). Antifungal effect of volatile organic compounds produced by *Pseudomonas chlororaphis* subsp. *aureofaciens* SPS-41 on oxidative stress and mitochondrial dysfunction of *Ceratomyces fimbriata*. *Pestic. Biochem. Physiol.* 173:104777. doi: 10.1016/j.pestbp.2021.104777
- Zhang, H., Liu, Y., and Wang, G. (2019). Integrated use of maize bran residue for one-step phosphate bio-fertilizer production. *Appl. Biochem. Biotechnol.* 187, 1475–1487. doi: 10.1007/s12010-018-2874-4
- Zhang, Q., Stummer, B. E., Guo, Q., Zhang, W., Zhang, X., Zhang, L., et al. (2021a). Quantification of *Pseudomonas protegens* FD6 and *Bacillus subtilis* NCD-2 in soil and the wheat rhizosphere and suppression of root pathogenic *Rhizoctonia solani* AG-8. *Biol. Control* 154:104504. doi: 10.1016/j.biocontrol.2020.104504
- Zhang, S., and Zhang, X. (2009). Effects of two composted plant pesticide residues, incorporated with *Trichoderma viride* on root-knot nematode in Balloonflower. *Agric. Sci. China* 8, 447–454. doi: 10.1016/S1671-2927(08)60231-X
- Zhao, X., Zhao, X., Wei, Y., Shang, Q., and Liu, Z. (2013). Isolation and identification of a novel antifungal protein from a rhizobacterium *Bacillus subtilis* strain F3. *J. Phytopathol.* 161, 43–48. doi: 10.1111/jph.12015