

MINIREVIEW

Plant Growth-Promoting Microorganisms as agents of biological control: Mechanisms and perspectives for sustainable plant protection

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ABSTRACT Plant growth-promoting microorganisms (PGPM), including plant growth-promoting bacteria (PGPB) and plant growth-promoting fungi (PGPF), can improve plant performance while simultaneously suppressing plant pathogens. Most PGPM colonize the rhizosphere, and some are also able to establish endophytic populations within plant tissues, where they contribute to plant health through direct antagonism, induced systemic resistance, improved nutrient acquisition, and phytohormone-related effects. These properties make PGPM attractive alternatives or complements to conventional pesticides in sustainable plant protection. This mini-review summarizes the principal mechanisms by which PGPM suppress pathogens, with particular emphasis on antimicrobial secondary metabolites, siderophore production, extracellular hydrolytic enzymes, mycoparasitism, mycophagy, and induced systemic resistance. In addition, nutrient mobilization and microbial phytohormone production are discussed as indirect but important contributors to disease reduction and plant vigor. Overall, PGPM-based approaches provide a multifunctional framework for sustainable plant protection by integrating direct pathogen suppression with improved plant performance and defense.

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Introduction

Plant growth-promoting microorganisms (PGPM) comprise a broad group of beneficial bacteria and fungi associated with plants, mainly their roots and the surrounding soil. They include plant growth-promoting bacteria (PGPB) and plant growth-promoting fungi (PGPF), most of which are actively colonizing the rhizosphere and are likely associated with most plant species across diverse environments (Baron and Rigobelo 2022; Compant et al. 2005). Some of these microorganisms are also able to enter internal root tissues, cross the endodermal barrier, and establish endophytic populations in stems, leaves, tubers, and other organs, where they persist in close association with the host plant (Kumar et al. 2012; Lodewyckx et al. 2002; Mercado-Flores et al. 2014; Santoyo et al. 2016).

The importance of PGPM lies in their dual function. On the one hand, they can directly stimulate plant growth through nutrient mobilization and phytohormone production; on the other hand, they may indirectly improve plant health by suppressing pathogens and priming host defenses (Bouizgarne 2013). These combined activities make PGPM attractive alternatives to conventional chemical

pesticides and valuable tools for sustainable disease management (Baron and Rigobelo 2022). Their suppressive effects rely on several overlapping mechanisms, including antibiosis, competition for nutrients and niches, mycoparasitism, mycophagy, and induced systemic resistance (Glick 2012; Mesanza et al. 2016; Pérez-Montañón et al. 2014). In this mini-review, we focus primarily on those PGPM traits that contribute directly or indirectly to biological control (Fig. 1).

Major mechanisms of PGPM-mediated biological control

Antagonism can be defined as a negative interaction in which one microorganism adversely affects the life processes of another organism inhabiting the same ecological niche. In microbial biocontrol, the principal forms of antagonism include antibiosis, competition and parasitism (Mesanza et al. 2016). It has been estimated that 1-35% of microorganisms isolated from the rhizosphere show antagonistic activity against plant pathogens (Berg 2009). In PGPM, antagonism is often based on the production of metabolites or enzymes that directly inhibit

PGPM-mediated biological control

beneficial bacteria and fungi link direct antagonism with plant growth and defense

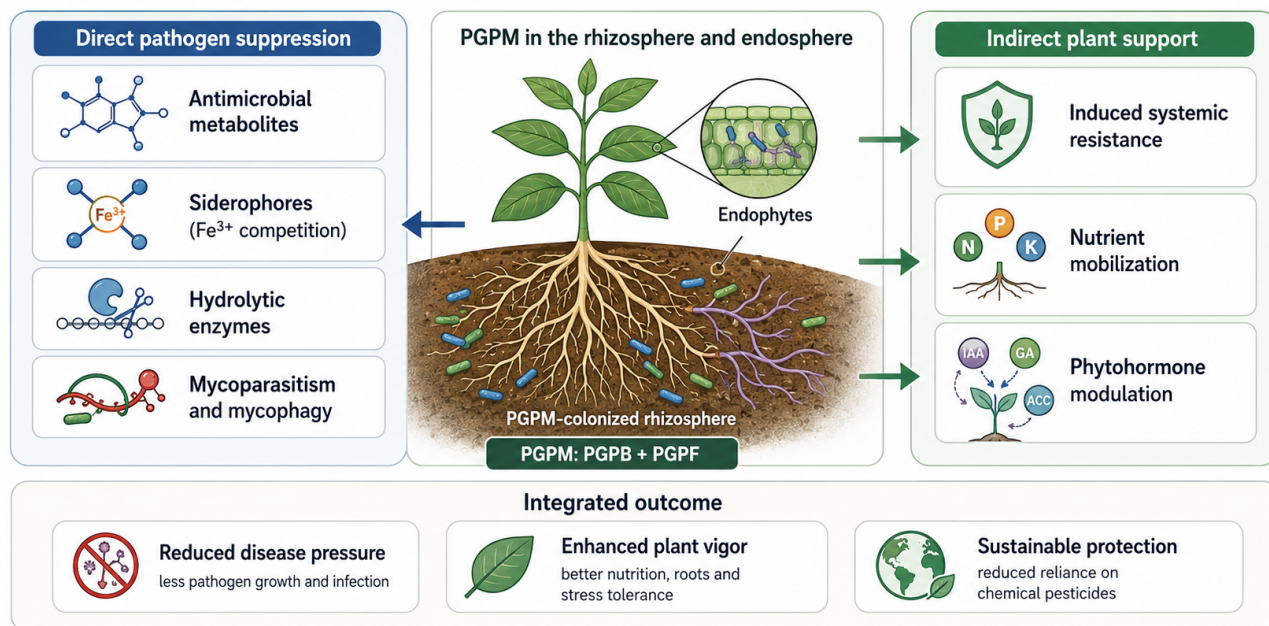


Figure 1. Schematic overview of the main direct and indirect mechanisms by which plant growth-promoting microorganisms (PGPM), including plant growth-promoting bacteria and fungi, contribute to biological control and sustainable plant protection.

pathogen growth and survival (Abhilash et al. 2016; Latz et al. 2018; Zhang et al. 2012).

Antimicrobial secondary metabolites

Antibiotics are low-molecular-weight organic compounds that negatively affect the growth and metabolism of susceptible microorganisms (Duffy et al. 2003; Glick and Bashan 1997). Their mechanisms of action are diverse and include inhibition of cell wall synthesis, disruption of cell membrane integrity, and interference with protein synthesis (Maksimov et al. 2011). PGPM produce a wide range of bioactive secondary metabolites, including alkaloids, steroids, terpenoids, peptides, polyketides, flavonoids, quinolones, phenolics, chlorinated compounds and volatile organic compounds, many of which display antibacterial, antifungal, antiviral or insecticidal activities (Baron and Rigobelo 2022; Lugtenberg et al. 2016).

Among bacteria, *Bacillus* and *Pseudomonas* species are among the most intensively studied natural producers of agriculturally relevant antibiotics (Beneduzi et al. 2012; Haas and Défago 2005). *Bacillus* spp. are especially well known for lipopeptide production. These cyclic compounds, typically composed of a short peptide linked to a beta-hydroxy fatty acid chain, have surfactant properties, high stability and strong affinity for lipid bilayers, allowing

them to damage biological membranes (Dimkić et al. 2015; Kumar et al. 2015; Maksimov et al. 2020; Ongena and Jacques 2008; Zhao et al. 2017). The best-known *Bacillus* lipopeptide groups are surfactins, iturins, and fengycins (Dimkić et al. 2015; Ongena and Jacques 2008; Raaijmakers et al. 2010; Wang et al. 2015). Iturins and fengycins are primarily antifungal, whereas surfactins also display antibacterial and antiviral activities and can contribute to root colonization and induced systemic resistance (Gond et al. 2015; Malviya et al. 2020; Ongena and Jacques 2008; Romero et al. 2007). *Bacillus* species may additionally produce polymyxin, bacitracin, mycosubtilin and bacillomycin, further widening their antagonistic potential (Chowdhury et al. 2015; El Arbi et al. 2015; Ongena and Jacques 2008; Torres et al. 2016).

Pseudomonas spp. also synthesize a broad spectrum of antagonistic secondary metabolites. Particularly important compounds include phloroglucinols, pyoluteorin, phenazines, pyrrolnitrins, and cyclic lipopeptides (Höfte and Altier 2010). Phenazines are redox-active nitrogen-containing heterocyclic antibiotics that can inhibit DNA replication, disrupt electron transport, impair membrane function and alter energy production in target microorganisms (Dimkić et al. 2022; Sreejith et al. 2019). Another key compound is 2,4-diacetylphloroglucinol (2,4-DAPG), which has strong antifungal activity and may also suppress

bacteria and viruses while contributing to host defense activation (Haas and Défago 2005; Tabassum et al. 2017).

Trichoderma species represent an important group of PGPF with well-documented antagonistic secondary metabolism. Metabolic preferences show broad saprotrophic versatility and universal adaptation to mycoparasitism and habitats such as arboreal microbial mats (Steindorff et al. 2026). Many of their bioactive compounds are thought to function in competition with other microorganisms for space and nutrients, and several of these metabolites are associated with membrane-targeting effects (Kubicek et al. 2019; Degenkolb et al. 2015). *Trichoderma* strains produce a diverse array of antimicrobial secondary metabolites that contribute substantially to their antagonistic activity against phytopathogens (Schirmböck et al. 1994; Vinale et al. 2006; Khan et al. 2020). Koniginin A is a polyketide-type metabolite originally described from *T. koningii* (Cutler et al. 1989). In addition, anthraquinones produced by *Trichoderma* species are primarily associated with pigmentation but may also exert antibacterial effects, whereas pyrones such as 6-pentyl- α -pyrone have been linked to growth inhibition of several plant-pathogenic microorganisms (Reino et al. 2008).

A particularly important group of *Trichoderma* metabolites is the peptaibiotics, which account for a large proportion of the secondary metabolites reported from these fungi (Röhrich et al. 2014). These membrane-active peptides, including the peptaibols, are characterized by amphipathic structures that enable them to form ion channels in biological membranes. As a result, they may inhibit mainly fungi and Gram-positive bacteria, and in some cases Gram-negative bacteria, through membrane permeabilization (Degenkolb et al. 2003; Degenkolb and Brückner 2008; Neumann et al. 2015; Pereira-Dias et al. 2023). Because of these properties, peptaibiotics are regarded as important contributors to the biocontrol potential of *Trichoderma*.

Species of the genus *Chaetomium* also represent an important source of antimicrobial metabolites. This genus includes numerous soil-inhabiting and endophytic taxa capable of producing a wide range of bioactive compounds, including chaetoglobosins, xanthonones, anthraquinones, azaphilones, terpenoids, and steroids (Li et al. 2011; Madbouly and Abdel-Wareth 2020; Wang et al. 2014; Zhang et al. 2012). Among them, *Chaetomium globosum* has attracted particular attention as a potential biocontrol fungus because of its fungicidal activity and multiple antagonistic traits (Linkies et al. 2020). Chaetoglobosins and related cytochalasans are especially noteworthy owing to their broad spectrum of bioactivities, including antifungal and antibacterial effects (Chen et al. 2016; Chen et al. 2020; Zhang et al. 2013).

Siderophore production

Iron is essential for all living organisms and plays a central role in chlorophyll synthesis, electron transport and a number of enzyme systems in plants (Shahwar et al. 2023; Sujatha and Ammani 2013). However, under natural conditions iron is often present as ferric iron (Fe^{3+}), which is poorly soluble and therefore not readily bioavailable. To overcome this limitation, many microorganisms produce siderophores, low-molecular-weight compounds with exceptionally high affinity for Fe^{3+} (Ali and Vidhale 2013; Beneduzi et al. 2012; Orozco-Mosqueda et al. 2021).

Under iron-deficient conditions, microorganisms release siderophores into the environment, where they chelate ferric iron and form soluble complexes that are recognized by specific receptors at the cell surface. The iron-siderophore complex is then transported into the cell, where iron is released and used metabolically. Catecholate-, hydroxamate- and carboxylate-type siderophores represent the major structural classes (Ali and Vidhale 2013). In the rhizosphere, siderophore production may suppress pathogens by depriving them of iron, thereby reducing their growth and competitiveness near plant roots (Ambrosini and Passaglia 2017; Beneduzi et al. 2012; Miethke and Marahiel 2007). At the same time, plants may also benefit because several studies have shown that they are able to acquire iron from microbial siderophore complexes (Sharma et al. 2003; Vansuyt et al. 2007; Yehuda et al. 1996).

Siderophore production has been reported from numerous bacterial genera, including *Pseudomonas*, *Azotobacter*, *Bacillus*, *Enterobacter*, *Serratia*, *Azospirillum*, *Rhizobium* (Saharan and Nehra 2011), *Dickeya* (Sandy and Butler 2011), *Methylobacterium* (Juma et al. 2022), *Streptomyces*, *Nocardia*, *Pantoea*, *Paenibacillus*, and *Rhodococcus* (Timofeeva et al. 2022). It is also widespread among fungi, such as *Chaetomium*, *Trichoderma*, *Aspergillus*, *Pochonia*, *Purpleocillium*, *Metarhizium*, and *Beauveria* species (Chen et al. 2019; Farias et al. 2018; Haruma et al. 2022; Usha and Padmavathi 2015; Wang et al. 2023; Yadav et al. 2017).

Extracellular enzymes

Many biocontrol microorganisms produce extracellular cell wall-degrading enzymes, including glucanases, chitinases, proteases and lipases, which contribute to the breakdown of pathogen cell walls (Cawoy et al. 2011; Chandrasekaran et al. 2012; Glick and Bashan 1997). Because fungal cell walls contain glycoproteins, chitin and beta-glucans, enzymes such as chitinases and beta-1,3-glucanases are particularly important in antagonism against fungal pathogens (Dimkić et al. 2022; Reddy et al. 2022; Santoyo et al. 2021).

Chitinases have been detected in numerous bacterial

taxa, including *Aeromonas*, *Bacillus*, *Chromobacterium*, *Enterobacter*, *Paenibacillus*, *Streptomyces*, *Pseudomonas*, *Rhizobium*, and *Serratia*. Within *Bacillus*, species such as *B. amyloliquefaciens*, *B. cereus*, *B. licheniformis*, *B. subtilis*, and *B. velezensis* are among the reported producers (Berini et al. 2018; Ghasemi and Ahmadian 2010; Sharma et al. 2011; Shrestha et al. 2015). Fungal chitinase producers include *Aspergillus*, *Beauveria*, *Clonostachys*, *Penicillium*, *Trichoderma*, and *Chaetomium* species, and these enzymes are often crucial for mycoparasitic behavior (Berini et al. 2018; Liu et al. 2008; Sharma et al. 2011; Singh and Seneviratne 2017).

Cellulases and xylanases also deserve attention. Cellulolytic enzymes can contribute not only to antagonism against oomycetous fungal pathogens but also to colonization of plant tissues and decomposition of plant residues, thereby improving nutrient cycling and reducing pathogen inoculum in soil (Darwish and Abdel-Azeem 2020; Reddy et al. 2022; Singh et al. 2020). Cellulase production is widespread among bacteria such as *Pseudomonas*, *Cellulomonas* and *Bacillus* species, and among fungi from the genera *Aspergillus*, *Penicillium*, *Fusarium*, *Chaetomium*, and *Trichoderma* (Chen et al. 2019; Singh et al. 2020). Xylanases are similarly common in *Bacillus* and *Trichoderma* species and may also act as elicitors of plant immunity (Okeke and Lu 2011; Singh et al. 2019; Devi et al. 2020).

Mycoparasitism

Mycoparasitism is a direct form of fungal antagonism in which a beneficial fungus recognizes, contacts, and attacks another fungus through hyphal attachment, coiling, penetration, and subsequent degradation of host structures (Viterbo and Horwitz 2010; Hasan et al. 2022). This process is typically supported by the secretion of cell wall-degrading enzymes, including chitinases, glucanases, cellulases, xylanases, and proteases, often acting together with antifungal secondary metabolites (Mukherjee et al. 2022). Among plant-associated fungi, *Trichoderma* species are the best-documented mycoparasites of phytopathogenic fungi. They are well known to coil around pathogen hyphae, penetrate them, and cause structural disintegration, while producing lytic enzymes such as β -1,3-endoglucanases, chitinases, and subtilisin-like proteases that contribute to host cell wall breakdown. In addition, proteins such as Epl-1 from *T. harzianum* may facilitate hyphal interaction with the pathogen and modulate virulence during mycoparasitic contact (Gomes et al. 2015; Gomes et al. 2017).

Mycophagy

Bacterial mycophagy refers to the ability of bacteria to feed on living fungi and convert fungal biomass into

bacterial biomass. Leveau and Preston (2008) described mycophagy as a set of phenotypic behaviors allowing bacteria to obtain nutrients from living fungal hosts. They distinguished necrotrophy, extracellular biotrophy and endocellular biotrophy as principal strategies. In necrotrophy, bacteria kill fungal cells through secreted toxins or enzymes and then exploit the liberated nutrients. In extracellular biotrophy, bacteria remain closely associated with living fungi, often at their surfaces, and utilize exuded compounds. In endocellular biotrophy, bacteria invade living fungal cells and draw nutrients directly from the cytoplasm (Leveau and Preston 2008).

In practice, mycophagy is often supported by a combination of toxins and hydrolytic enzymes. Bacterial toxins may first inhibit or kill fungal cells, after which chitinases, lipases, glucanases and proteases participate in the degradation and assimilation of fungal polymers. These exoenzymes may act synergistically with toxic metabolites to enhance antifungal activity (Someya et al. 2007; Woo et al. 2002). *Collimonas fungivorans* is one of the best-known mycophagous bacteria, but mycophagy-related behavior has also been described in *Serratia marcescens*, *Bacillus cereus*, *B. megaterium*, *B. thuringiensis*, *Pseudomonas* spp., *Burkholderia* spp., *Paenibacillus* spp., *Staphylococcus aureus*, and *Streptomyces* spp. (Deveau et al. 2018; Leveau and Preston 2008).

Induced systemic resistance

Besides direct antagonism, PGPM may also protect plants by induced systemic resistance (ISR), which is a plant-wide enhanced defensive state triggered by beneficial microorganisms after local interaction with the host. In contrast to pathogen-induced systemic acquired resistance (SAR), PGPM-mediated ISR is commonly associated with jasmonic acid and ethylene signaling rather than salicylic acid-dependent cell death responses (Jha et al. 2012; Mercado-Flores et al. 2014; Santoyo et al. 2016). The result is a primed plant that responds more rapidly and effectively to later pathogen attack.

Among bacteria, *Bacillus* species are prominent ISR elicitors. Reports have documented ISR-related activity in *B. amyloliquefaciens*, *B. subtilis*, *B. pasteurii*, *B. cereus*, *B. pumilus*, *B. mycoides*, and *B. sphaericus* (Kloepper et al. 2004; Raaijmakers et al. 2010; Ryu et al. 2004). In these bacteria, lipopeptides such as surfactin and fengycin may function not only as antimicrobials but also as elicitors of systemic defense (Ongena and Jacques 2008). *Pseudomonas* species are similarly important. In particular, *P. fluorescens* and *P. putida* have been reported to protect plants against pathogens such as *Colletotrichum falcatum*, *Ceratocystis fagacearum*, and *Fusarium oxysporum* (Compant et al. 2005). In addition to jasmonate signaling, volatile compounds such as 2R,3R-butanediol have been

implicated in ISR induction by *Pseudomonas* in tobacco (Han et al. 2006). Certain siderophores also act as ISR elicitors; pseudobactin (pyoverdine/fluorescein) produced by *P. putida* has been shown to induce resistance against several pathogens in eucalyptus, tomato, and tobacco (De Vleeschauwer and Höfte 2009; Meziane et al. 2005; Ran et al. 2005; Van Loon et al. 2008).

PGPF are likewise able to elicit host defenses. In *Trichoderma*, root colonization may involve appressorium-like structures and penetration of root cortical tissues, which stimulates neighboring plant cells to synthesize new cell walls and phenolic compounds (Shoresh et al. 2010). Enzymatic proteins such as xylanases and cellulases, as well as other peptides and small proteins, have been identified as fungal ISR elicitors (Pieterse et al. 2014). ISR-eliciting fungal genera include *Trichoderma*, *Fusarium*, *Penicillium*, *Phoma*, and *Chaetomium* (Elshahawy and Khattab 2022; Elsharkawy et al. 2012; Gajera et al. 2013; Hossain et al. 2007; Koike et al. 2001; Segarra et al. 2009).

Because *Trichoderma* species frequently interact with plants in soil, the effects of peptaibols on host physiology have also attracted attention. In addition to antimicrobial activity, some peptaibols may influence plant hormonal pathways and alter plasma membrane or mitochondrial membrane permeability (Matic et al. 2005; Rippa et al. 2010). Several studies suggest that these metabolites can also contribute to ISR (Yadav and Khare 2025). Peptaibols produced by *T. virens* enhanced systemic resistance in cucumber against *Pseudomonas syringae* pv. *lachrymans* (Viterbo et al. 2007), while peptaibols from *T. harzianum* increased defense responses against cucumber mosaic virus (Kai et al. 2018). Trichokonins produced by *T. pseudokoningii* are also known to induce systemic resistance in tobacco against tobacco mosaic virus through activation of multiple defense mechanisms (Luo et al. 2010). More recently, peptaibols produced by *T. longibrachiatum* were reported to reduce fruit brown rot caused by *Monilia yunnanensis* in pear (*Pyrus bretschneideri*) (Lv et al. 2024).

Growth-promoting functions linked to disease suppression

Nutrient mobilization

The growth-promoting effects of PGPM are tightly connected to disease suppression because nutritionally stronger plants are often more resilient. Nitrogen fixation is one of the classic examples. Nitrogen is indispensable for the synthesis of proteins, chlorophyll and nucleic acids, yet plant-available forms of nitrogen are often limited in soil (Hayat et al. 2010). Atmospheric N₂ can be

fixed by both symbiotic and free-living microorganisms. Symbiotic diazotrophs such as *Rhizobium* and *Bradyrhizobium* establish nodules on the roots of suitable host plants, whereas free-living or associative nitrogen fixers may interact more loosely with crops such as wheat and maize (Lugtenberg and Kamilova 2009). Reported free-living or associative nitrogen-fixing taxa include *Azospirillum*, *Azoarcus*, *Azotobacter*, *Acetobacter*, *Bacillus*, and *Pseudomonas* (Pérez-Montaña et al. 2014; Saharan and Nehra 2011).

Phosphorus mobilization is another key trait of plant growth promotion. Although soils often contain substantial amounts of total phosphorus, most of it occurs in poorly available organic or inorganic forms, whereas the directly absorbable fraction may be very low (Ahemad and Kibret 2014; Glick 2012; Hayat et al. 2010). Many soil microorganisms can solubilize mineral phosphates or mineralize organic phosphorus through acidification, chelation, or enzyme production, including phosphatases, phytases, and C-P lyases (Pérez-Montaña et al. 2014; Saxena et al. 2020). Representative bacterial phosphorus mobilizers include species of *Bacillus*, *Pseudomonas*, *Azospirillum*, *Rhizobium*, *Serratia*, *Burkholderia*, *Azotobacter*, *Enterobacter*, and *Microbacterium* (Bhattacharyya and Jha 2012; Pérez-Montaña et al. 2014; Tagore et al. 2013). Fungal genera such as *Chaetomium*, *Aspergillus*, *Penicillium*, and *Trichoderma* have also been reported as effective phosphorus mobilizers (Khan et al. 2010; Rawat et al. 2021; Tarafdar and Gharu 2006). By improving phosphorus availability, these microorganisms may strengthen root development and plant vigor, thereby indirectly reducing disease susceptibility.

Phytohormone production and modulation

PGPM also influence plant growth and stress responses through phytohormone production or modulation. Among these compounds, indole-3-acetic acid (IAA) is the most frequently discussed microbial auxin. Auxin regulates cell elongation, cell division, differentiation, root initiation and apical dominance, and it is also involved in plant responses to abiotic and biotic stresses (Mohite 2013). Many rhizosphere bacteria are capable of IAA production; estimates suggest that roughly 80% of bacteria isolated from the root zone may synthesize this compound (Gupta et al. 2015; Hayat et al. 2010). Examples include *Bacillus subtilis*, *B. licheniformis*, *Azotobacter* spp., *Paenibacillus* spp., and *Pseudomonas* spp. (Bhattacharyya and Jha 2012; Bouizgarne 2013; Tsavkelova et al. 2007). IAA production is also known from several fungi, including *Aspergillus*, *Mortierella*, *Talaromyces*, *Fusarium*, *Penicillium*, *Trichoderma*, and *Chaetomium* species (Khan et al. 2012; Sarkar et al. 2022; Syamsia et al. 2021; Tian et al. 2022).

Absciscic acid (ABA) is another relevant hormone because

it is closely linked to abiotic stress tolerance. Certain PGPR can synthesize ABA or alter plant ABA homeostasis, thereby affecting stomatal conductance, ion uptake, root growth, and overall tolerance to stress conditions (Belimov et al. 2014; Sah et al. 2016). Reported examples include *Azospirillum brasilense*, *Herbaspirillum seropedicae*, *Bacillus licheniformis*, *Pseudomonas fluorescens*, *B. subtilis*, *Arthrobacter protophormiae*, *P. putida*, and *Novosphingobium* sp. (Barnawal et al. 2017; Cohen et al. 2015; Curá et al. 2017; Salomon et al. 2014; Shahzad et al. 2013; Vives-Peris et al. 2018).

Ethylene and cytokinins are also important components of the PGPM effect. Although many bacteria produce ethylene, excessive ethylene can inhibit seed germination and root elongation. Accordingly, an important plant-beneficial trait of many PGPR is the reduction of stress ethylene levels rather than their enhancement (Hayat et al. 2010; Iqbal et al. 2017; Wani et al. 2016). The enzyme **ACC deaminase** reduces the level of stress ethylene by degrading its precursor, 1-aminocyclopropane-1-carboxylate (ACC), into ammonia and alpha-ketobutyrate. Since excessive ethylene production under stress conditions can restrict root growth and weaken plant performance, ACC deaminase-producing microorganisms may enhance plant tolerance to both abiotic stress and pathogen attack, indirectly contributing to disease reduction and improved plant fitness (Glick 2012; Jha et al. 2012; Zhang et al. 2011; Shahzad et al. 2013). Cytokinins, which regulate cell division and delay leaf senescence, have been reported from a wide range of rhizosphere microorganisms, including *Azotobacter* spp., *Rhizobium* spp., *Pantoea agglomerans*, *Rhodospirillum rubrum*, *Pseudomonas fluorescens*, *Bacillus subtilis*, and *Paenibacillus polymyxa* (Egamberdieva et al. 2017; Glick 2012; Hayat et al. 2010; Schmülling 2002).

Some microorganisms, especially *Azospirillum* spp., can also produce gibberellins, thereby influencing stem elongation, seed development and flowering-related processes (Bhattacharyya and Jha 2012; Santner et al. 2009).

Conclusions

Plant growth-promoting microorganisms offer a multi-functional framework for biological control because they combine direct antagonism with indirect enhancement of host vigor and defense capacity. Antimicrobial secondary metabolites, siderophore production, extracellular hydrolytic enzymes, mycoparasitism, mycophagy, and induced systemic resistance all contribute to pathogen suppression, while nitrogen fixation, phosphorus mobilization, and phytohormone-related effects support plant

performance under stress. Their practical value lies not only in their inhibitory activity against pathogens but also in their capacity to improve plant health and prime resistance.

Despite this considerable potential, the successful application of PGPM in sustainable plant protection still faces important challenges. Future work should focus on the selection of well-adapted strains, clarification of their dominant mechanisms under field conditions, improvement of formulation stability and shelf life, and evaluation of colonization consistency across different crops and environments. In addition, a better understanding of the interactions between introduced PGPM and resident microbiota, together with regulatory and biosafety considerations, will be essential for the reliable and large-scale implementation of PGPM-based biocontrol strategies.

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