

Secondary metabolites of *Pseudomonas* and *Bacillus* species in plant disease management

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Abstract: Beneficial *Pseudomonas* spp. and *Bacillus* spp. are ubiquitous in soils and colonize the plant microbiome, including the rhizosphere, phyllosphere, and endosphere. Their beneficial effects on host plants are due to a wide range of secondary metabolites that act through several mechanisms, including direct antibiosis (antifungal, antibacterial, antiviral, and antinematicidal), competition for nutrients, promotion of plant growth and the induction of systemic resistance (ISR) in host plants. The genus *Pseudomonas* includes a variety of species with beneficial effects on plant health that play an important role in sustainable agriculture. The major secondary metabolites involved in biocontrol are phenazine-1-carboxylic acid, phenazine-1-carboxamide, pyrrolnitrin, pyoluteorin, 2,4-diacetylphloroglucinol, nunamycin, nunapeptin, brasmycin, braspeptin, sessilins, orfamides, HCN and various volatile organic compounds. Competition for nutrients, such as iron uptake, is based on siderophores such as pyoverdine and pyochelin. Plant-growth promotion is mediated by 1-aminocyclopropane-1-carboxylate deaminase, indoleacetic acid, abscisic acid, gibberellic acid, and cytokinins, as well as vitamins niacin, pantothenic acid, thiamine, riboflavin, and biotin. Endospore-forming *Bacillus* species also inhibit phytopathogens, including all of the above mechanisms underlined by a wide range of structurally diverse compounds. Direct inhibition of vast variety of phytopathogens is achieved by compounds such as volatiles, bacteriocins, and lipopeptides, i.e., iturins, surfactins, fengycins, and kurstakins. Indirect effects are performed by phytostimulating compounds such as auxins, gibberellins, cytokinins and abscisic acid, which positively influence plant growth and development. They also induce systemic resistance in the host plant through the production of volatiles. Expression of defense-related proteins is induced in plants by lipopeptides, polyketides, and volatiles that

activate the jasmonic acid, salicylic acid, or ethylene signaling pathways. They also have the ability to inhibit quorum sensing of various phytopathogens. As a result, higher biomass and nutritional quality, improved nutrient mobilization and uptake, enhanced tolerance to biotic and abiotic stresses, and shaping of the microbiota are all positive effects that healthy plants acquire from *Pseudomonas* and *Bacillus* beneficial strains. This review aims to highlight the most important aspects of *Pseudomonas* spp. and *Bacillus* spp. secondary metabolites in the control of phytopathogens and their beneficial properties for the host plant. Bioformulations based on their metabolites could replace synthetic pesticides and enable sustainable agricultural practices.

Keywords: *Bacillus*; *Pseudomonas*; biological control; plant growth-promoting; secondary metabolites

1. Introduction

Biocontrol represents the suppression of pathogenic species by introducing of their natural enemies and/or their secondary metabolites. In agriculture, these biological control agents (BCAs) can be used as substitutes for various chemical pesticides including bactericides and fungicides to obtain more eco-friendly plant health management methods that wouldn't cause harm to the environment or human welfare. Biocontrol can also be used when pathogenic species develop resistance to conventional chemical agents or, for instance, when chemical agents are not available to control a particular plant disease (Fravel, 2005). Agriculturally important BCAs are commonly identified as representatives of the genera *Bacillus* and *Pseudomonas*. They produce secondary metabolites with great potential to combat a wide variety of phytopathogens. In addition, these metabolites have shown the capacity for growth promotion of plants

associated with microorganisms synthesize them (Fravel, 2005; Manikandan *et al.* 2023). An overview of *Bacillus* spp. and *Pseudomonas* spp. as BCAs on plants is shown in Figure 1.

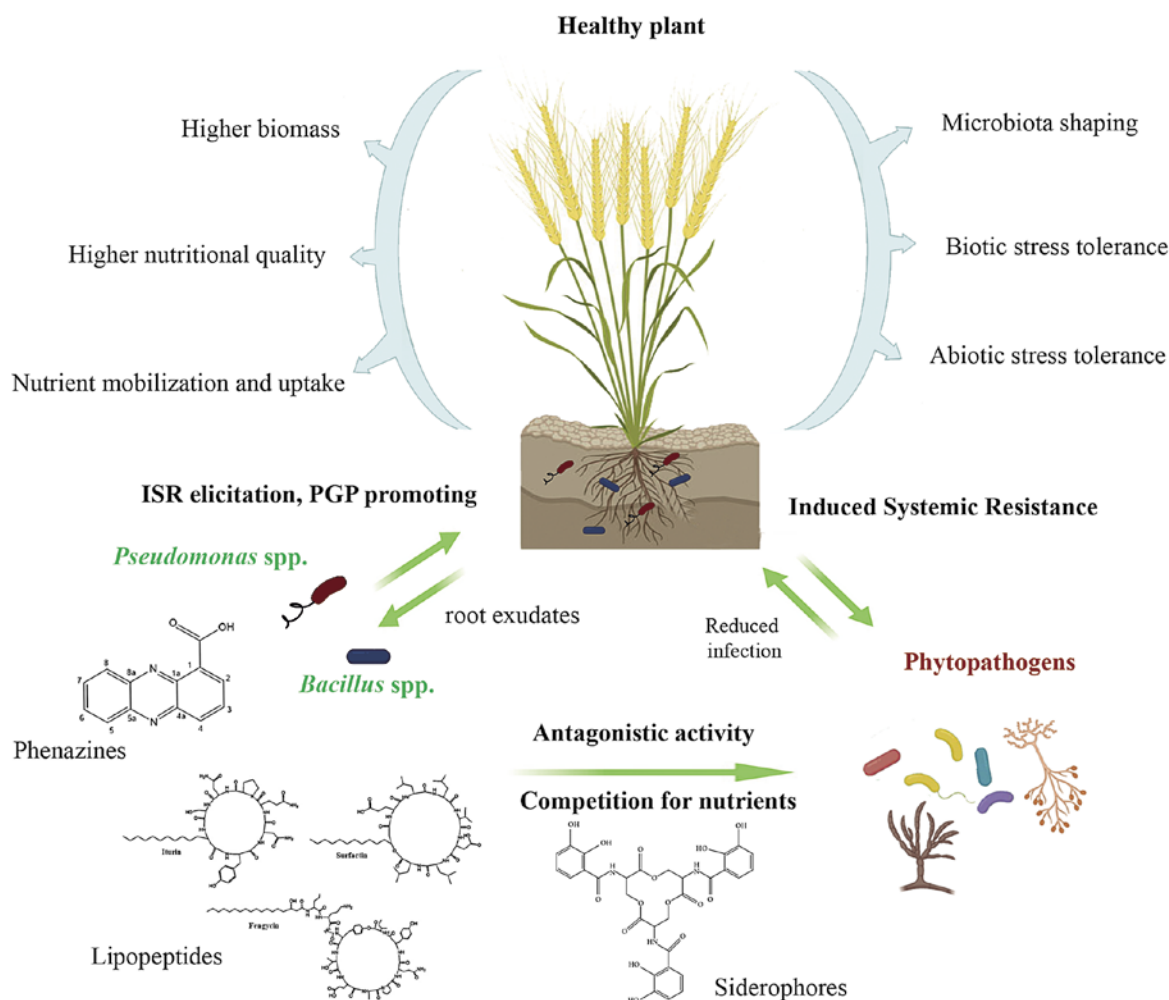
The main characteristics of BCAs are their high specificity to target plant pathogens, easy degradation, and low cost of mass production. Biocontrol microbes use different approaches to identify and neutralize their target, i.e., phytopathogens. These approaches include competition for resources, hyperparasitism, antibiosis and induction of systemic resistance in host plants (Živković *et al.* 2010). Biocontrol by competition for resources, whether for ecological niches or nutrients, is the limitation of pathogenic species fitness through the use of limited resources by biocontrol microbes that outcompete them (Hibbing *et al.* 2010). Hyperparasitism is the ability of biocontrol to reduce pathogen population by parasitizing them, while antibiotics or toxins

production generally mediates antibiosis by the antagonist, which can inhibit pathogen proliferation (Pankhurst & Lynch, 2005; Rani *et al.* 2020). Induction of systemic resistance by BCAs is the process by which they activate a plant's physical or chemical barriers that protect it from phytopathogens. Induced resistance has been accomplished in plants through the colonization of roots by BCA strains. Once the community of BCA strains is established in the roots, plants are much more likely to resist colonization by pathogenic strains (Martinuz *et al.* 2012).

2. *Pseudomonas* species in biocontrol

Pseudomonas is a genus of non-spore-forming, Gram-negative, rod-shaped bacteria, found in a variety of habitats, including bulk soil and rhizosphere. *Pseudomonas* species use various substrates as nutrients and survive in different conditions that would be stressful for other bacteria. Therefore, they grow rapidly, adapt, and colonize different types of soil, including disease-suppressive soils (Weller, 2007). Considering ecological niches,

Figure 1. Plant growth-promoting and biocontrol mechanisms of beneficial *Pseudomonas* and *Bacillus* strains and their effects on plant health.



Pseudomonas spp. is a highly successful colonizer in the rhizosphere, particularly in nutrient-poor soils. These soils have an effective excess of carbon because the plants are restricted in their growth by nutrient limitation and therefore cannot assimilate all available carbon (Lugtenberg *et al.* 2001; Tuomi *et al.* 1984). It has been determined that motility, production of the O-antigen of lipopolysaccharide (LPS), cellulose, thiamine, amino acids, and biotin, as well as the synthesis of an isoflavonoid-inducible efflux pump, are all essential points for effective colonization of the root and rhizosphere of the host plant (Lugtenberg *et al.* 2001). There is also evidence that *Pseudomonas* strains undergo genomic rearrangements in response to environmental changes that would allow better colonization of the rhizosphere (Martínez-Granero *et al.* 2005).

Many strains of *Pseudomonas* are known to produce versatile metabolites with plant growth-promoting (PGP) properties and the ability to induce systemic resistance in plants. Some of these compounds include the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which reduces ethylene levels in the root, thereby increasing root growth and length (Penrose & Glick, 2001); hormones such as indole acetic acid (IAA), abscisic acid (ABA), gibberellic acid (GA) and cytokinins (Dey *et al.* 2004; Dobbelaere *et al.* 2003; Patten & Glick, 2002); vitamins, namely niacin, pantothenic acid, thiamine, riboflavin and biotin (Revillas *et al.* 2000); cell-surface compounds (flagellin and lipopolysaccharides); and secondary metabolites such as lipopeptides, 2,4-diacetylphloroglucinol, siderophores, salicylic acid, pyochelin, pyocyanin, and volatile organic compounds (VOCs) (Audenaert *et al.* 2002; Park *et al.* 2015; Pieterse *et al.* 2014; Tran *et al.* 2007; Weller *et al.* 2012).

Considering the competition for nutrients, *Pseudomonas* species are very effective under iron-limiting conditions because they are able to synthesize iron-chelating compounds, i.e., siderophores. Since iron is present in proteins with [Fe-S] clusters and in heme, it is essential for different metabolic activities. One of the strategies for iron uptake is the binding of this micronutrient by iron-siderophore complexes, which have a high affinity for this molecule. This chelating and binding of iron by *Pseudomonas* spp. makes it less available to other microbes, including phytopathogens. Therefore, the synthesis of siderophores gives BCAs an important advantage in the competition for nutrients (Andrews *et al.* 2003). Among the high-affinity siderophores produced by fluorescent *Pseudomonas* spp. pyoverdines are highlighted as the main group. These green-yellow fluorescent pigments are synthesized by non-

ribosomal peptide synthetases (Visca *et al.* 2007). The mechanism of iron uptake under aerobic conditions, mediated by iron-pyoverdine complexes, occurs in several steps. The non-fluorescent pyoverdine precursor ferribactin is synthesized in the cytoplasm and transported via the ABC transporter PvdE to the periplasm, where chromatophore maturation occurs. After maturation, pyoverdine is exported to the extracellular matrix where it comes into contact with Fe³⁺ creating ferripyoverdine. Further, ferripyoverdine is taken up via the FpvA receptor, which is a large porin with 22 β -strands that form a gated β -barrel called the TonB-dependent outer membrane receptor. Because the N-terminal domain of the protein constricts the pore, the N-terminal end of the receptor contains a domain called the TonB box. This domain interacts with TonB, an inner membrane protein that, together with ExbB and ExbD, transfers the energy of the proton motive force to allow opening of the gate and transport of the ferric complex into the periplasm. In the periplasm, an iron ion is reduced and released, followed by recycling and excretion of apo-pyoverdine. Recycling and excretion of pyoverdine involves the efflux pump, which consists of three proteins, PvdT, PvdR, and OpmQ. While the ferripyoverdine-binding protein is common in other species, it was not observed in the periplasm of *Pseudomonas* strains. This implies that iron alone is transported into the cytoplasm (Andrews *et al.* 2003; Imperi *et al.* 2009; Visca *et al.* 2007). In addition to pyoverdine as the primary siderophore, almost all fluorescent *Pseudomonas* species produce secondary siderophores with low affinity that are structurally diverse. Some may be derived from peptides and they are synthesized by non-ribosomal peptide synthetases, such as pyochelin, pseudomonine, yersiniabactin, corrugatin, and ornicorrugatins, whereas achromobactin, quinolobactin, and thioquinolobactin are synthesized differently (Cornelis, 2010; Matthijs *et al.* 2007). It's estimated that these secondary siderophores are produced for energy conservation in situations where iron limitation is less drastic because the number of genes included for their biosynthesis is less than the number of genes for the synthesis of pyoverdine (Moon *et al.* 2008). Moreover, these siderophores have shown catalytic properties in some antibiosis mechanisms (Matthijs *et al.* 2007). An example of siderophore-mediated control of phytopathogens is the ability of *Pseudomonas syringae* pv. *syringae* to inhibit the growth of *P. syringae* pv. *glycinea*, Gram-negative bacterium that causes bacterial blight (Wensing *et al.* 2010).

Members of the genus *Pseudomonas* produce a wide range of antimicrobial compounds with the potential

to inhibit the growth of different phytopathogens. Some of these antimicrobials includes pyrazines, phenazine-1-carboxylic acid (PCA), phenazine-1-carboxamide, 2,4-diacetylphloroglucinol, pyrrol-nitrin, hydrogen cyanide (HCN), pyoluteorin and protein-type compounds (bacteriocins). Studies have shown that cyclic lipopeptides produced by *Pseudomonas* species, i.e., nunamycin, nunapeptin, brasmycin, and braspeptin are essential for antifungal activity, while sessilins and orfamides displayed additive roles in the suppressing some fungal diseases (Dimkić *et al.* 2022). Phenazine-1-carboxylic acid together with 4-acetamidobenzoic acid, 4-hydroxybenzoic acid, and 2-hydroxyphenyl nitrite extracted from *Pseudomonas synxantha* showed antifungal activity against *Monilinia laxa*, an ascomycete fungus responsible for brown rot disease infecting many different types of stone fruit (Janakiev *et al.* 2019). The same compound found in *Pseudomonas orientalis* X2-1P showed antibacterial properties against *Xanthomonas campestris* pv. *campestris*, a pathogenic bacterium that affecting the growth and quality of various cultivated *Brassicaceae* (Jelušić *et al.* 2021), while PCA from *Pseudomonas fluorescens* 2-79 shows protective and PGP properties against wheat infected by *Gaeumannomyces graminis* var. *tritici* (Thomashow & Weller, 1988). Pyocyanin is a toxic PCA-derived metabolite produced by *P. aeruginosa* that promotes the production of reactive oxygen species. It has antibacterial properties that increase fitness in competition with other bacterial species, as well as antifungal abilities against the oomycetes *P. myriotylum* and *Pythium* spp. and the filamentous fungi *Septoria tritici* and *Fusarium* spp. (Anjaiah *et al.* 1998; Flaishman *et al.* 1990; Tambong & Höfte, 2001).

Another important group of antimicrobials are VOCs, small molecules synthesized by primary and secondary metabolic pathways that include chemical classes such as alcohols, esters, aliphatic and aromatic hydrocarbons, terpenes, nitrogen, and sulfur compounds, and others. VOCs such as nonanal, benzothiazole, and 2-ethyl-1-hexanol, found in the bacterium *Pseudomonas chlororaphis* PA23, together with non-volatile antibiotics phenazine and pyrrolnitrin, are able to protect the phyllosphere of canola from the plant pathogenic fungus *Sclerotinia sclerotiorum*, which causes white mold disease (Fernando *et al.* 2007). VOCs such as 2,5-dimethylpyrazine, 2-methylpyrazine, 2-ethyl-5-methylpyrazine, 2-ethyl 3, 6-dimethylpyrazine and dimethyl trisulfide from *Pseudomonas putida* BP25 have antifungal activity against phytopathogenic fungi *Phytophthora capsici*, *Pythium myriotylum*, *Colletotrichum gloeosporioides*, *Rhizoctonia solani*,

Gibberella moniliformis, *Athelia rolfsii*, *Magnaporthe oryzae*, the bacterium *Ralstonia pseudosolanacearum*, and the plant-parasitic nematode *Radopholus similis* (Agisha *et al.* 2019).

Biocontrol mechanisms of *Pseudomonas* strains also include the production and extraction of HCN, a secondary metabolite that has antimicrobial properties. It has been shown that the bacterial strain *P. fluorescens* CHA0 can suppress black root rot of tobacco, a disease caused by the fungus *Thielaviopsis basicola*, by synthesising HCN in cooperation with other antifungal secondary metabolites (Voisard *et al.* 1989). Antifungal properties are also exhibited by the compound 2,4-diacetylphloroglucinol, which is extracted from different fluorescent *Pseudomonas* species, and can inhibit the growth of various fungal species (Weller *et al.* 2002).

3. *Bacillus* species in biocontrol

Bacillus is a genus of spore-forming, Gram-positive, rod-shaped bacteria with a very diverse secondary metabolism that allows the production of a wide range of structurally diverse compounds. For example, on average, about 4-5% of the whole genomes of *Bacillus subtilis* strains is dedicated to the synthesis of secondary metabolites (Stein, 2005). These compounds often have PGP properties that can manifest through direct or indirect mechanisms. Direct mechanisms include phyto-stimulating compounds that provide an advantage in competition for nutrients and ecological niches. Indirect approaches, on the other hand, include the synthesis and use of compounds, such as antimicrobials, that have an inhibitory effect on the pathogenic organism (Ahmad *et al.* 2008). Among phyto-stimulating compounds, plant hormones are of particular interest, as bacteria of the genus *Bacillus* have been found to be able to produce cytokinins, auxins, gibberellins, and abscisic acid, which positively influence plant growth and development (Arkhipova *et al.* 2007; Idriss *et al.* 2002; Joo *et al.* 2004; Xu *et al.* 2018). Other important phyto-stimulants include VOCs such as 2,3-butanediol and acetoin, which have been shown to be essential metabolites in chemical signal transduction between *B. strains* and *Arabidopsis thaliana* (Ryu *et al.* 2003). Although other volatile compounds, aldehydes, ketones, alcohols, 1-octen-3-ol and butyrolactone, have also been detected in chemical signaling, their role in plant development and plant-bacterial interactions has not been fully elucidated (Gutiérrez-Luna *et al.* 2010).

Bacillus strains are known for their ability to produce various antimicrobials, of which lipopeptides are the most important class. Their molecular

structure is predominantly rigid, hydrophobic, and cyclic, and consists of D-amino acids with high resistance to hydrolysis by peptidases and proteases. These antimicrobials are also resistant to oxidation thanks to their already oxidized structure and thioether bonds (Katz & Demain, 1977). There are two different pathways of lipopeptide biosynthesis. The first pathway is the non-ribosomal synthesis of peptides by large megaenzymes (NRPSs), while the second pathway is the ribosomal synthesis of linear precursor peptides that undergo post-translational modification and proteolytic processing (Stein, 2005).

Ribosomally synthesized antimicrobial lipopeptides are mainly small, heat-stable, amphiphilic proteins marked as bacteriocins. These compounds are produced by strains of specific microbial species and are effective against other closely related bacteria because their spectrum of inhibition is usually limited and their mechanism of action involves interaction with the wall of target cell (Field *et al.* 2007). *Bacillus* spp. bacteriocins can be classified into three groups. Class I includes peptides that undergo post-translational modification. The first three subclasses are considered lantibiotics because they are modified with lanthionine and b-methyl lanthionine; the fourth subclass has other posttranslational modifications. Based on their structure, two types of lantibiotics are described. Type A lantibiotics, which have a linear structure, are able to form voltage-dependent pores in the cytoplasmic membrane of Gram-positive target cells and destroy them. Gram-positive lantibiotic producers have special mechanisms of self-protection against their products. Immunity is based on export of the lantibiotic from the cytoplasmic membrane to the extracellular space, which occurs through the transporter proteins LanFEG, or on the membrane-bound lipoproteins LanI, which prevent lantibiotics from forming a lipid pore II and also prevent high local concentrations of the lantibiotic near the cytoplasmic membrane (Stein *et al.* 2005; Stein *et al.* 2003).

The bacteriocins of the class II belong to the small peptides synthesized ribosomally but not modified, which are heat stable. Large proteins with antibacterial activities based on their enzymatic activities are placed into class III. This group also includes peptides and proteins with antimicrobial properties that are not sufficiently defined to classify them, so they are generally referred to as bacteriocin-like inhibitory substances (BLIS) (Lodemann *et al.* 2008). Due to their limited inhibitory spectrum, *Bacillus* strains producing bacteriocin do not play a major role in biocontrol. However, non-ribosomally synthesized lipopeptides and peptides, such as

fengycins, iturins, surfactins, and kurstakins have shown great potential to control a variety of plant pathogens (Dimkić *et al.* 2013; Dimkić *et al.* 2017; Mishra *et al.* 2015).

Non-ribosomally synthesized peptides and lipopeptides are synthesized by non-ribosomal peptide synthetases (NRPSs), large multi-domain enzyme complexes with modular structure. They are a large, diverse group of compounds, including amino acids, and amino- or hydroxyl-fatty acids with hydrocarbon chains of varying lengths. They can be additionally modified by acylation, methylation, or glycosylation. The modular structure of megaenzymes is crucial for the process of amino-acid incorporation, as each module has several domains, including PCP (peptidyl carrier protein) and domain A, which is responsible for adenylation and thus activation of an amino acid (Fischbach & Walsh, 2006). The process of biosynthesis begins with the transfer of the phosphopantetheinyl group to the PCP (peptidyl carrier protein), catalyzed by the specific phosphopantetheinyl transferase and the activation of the amino acid. The activated amino acid is then transferred to the 4'-phosphopantetheine group of the PCP, resulting in the formation of a thioester bond. The C domain of a module is responsible for catalyzing the formation of a peptide bond between amino acids during polymerization. In addition, the E domain catalyzes the epimerization of certain amino acids since many non-ribosomal peptides contain D- and L- stereoisomers of amino acids. This property contributes to its resistance to the action of proteolytic enzymes (Fischbach & Walsh, 2006). Non-ribosomally synthesized antimicrobial lipopeptides from *Bacillus* species can be divided into four prominent families - iturins, surfactins, fengycins, and kurstakins. These cyclic lipopeptides consist of seven or ten amino acid residues linked to a fatty acid derivative. Due to the different lengths of the fatty acid hydrocarbon chains or the different composition of the amino acids, these molecules can assume many isomeric forms (Ongena & Jacques, 2008).

Lipopeptides from the iturin family are circular heptapeptides attached to a β -amino fatty acid chain with a length of 14 to 17 carbon atoms and exhibit high *in vitro* antifungal activity against various yeast and fungal strains but limited antibacterial and no antiviral activities. Iturin A and C, bacillomycin D, F, L, and LC and mycosubtilin are the seven major variants within the iturin family (Jacques, 2011; Ongena & Jacques, 2008). Iturin A, produced by various strains of *B. subtilis*, *B. amyloliquefaciens* and other *Bacillus* species, has plant-protective activity against many fungi such as *Phomopsis sclerotioidea*, *Fusarium oxysporum* f. sp. *radicis-lycopersici*,

Rosellinia necatrix, *Gloeosporium gloeosporioides*, *Alternaria mali*, *Botrytis elliptica*, *Botrytis cinerea*, *Colletotrichum musae*, *Sclerotium rolfsii*, *Glomerella cingulata*, *R. solani*, *Alternaria citri*, *C. gloeosporioides*, *Penicillium crustosum*, *F. graminearum* and *Pythium irregulare* (Arrebola *et al.* 2010; Cazorla *et al.* 2007; Cho *et al.* 2003; Hsieh *et al.* 2008; Kita *et al.* 2005; Zhao *et al.* 2014). Antibacterial activity manifested in suppression of *X. campestris* pv. *campestris*, growth has been demonstrated with a compound known as iturin A2 produced by *B. amyloliquefaciens*. In addition, iturins produced by *B. subtilis* suppress diseases caused by *X. campestris* pv. *cucurbitae* and *Pectobacterium carotovorum* subsp. *carotovorum* (Falardeau *et al.* 2013; Yoshida *et al.* 2001). Two bacillomycin D analogs produced by *B. subtilis* AU195 showed antifungal properties against *Aspergillus flavus*, while *B. amyloliquefaciens* exhibited potent antifungal activities against *R. solani* due to the production of bacillomycin L as well as bacillomycin D (Chowdhury *et al.* 2015; Li *et al.* 2014; Moyne *et al.* 2001). The fungicidal abilities of bacillomycin D were also confirmed against *F. graminearum*, *Alternaria alternata*, *Cryphonectria parasitica*, and *P. capsici* (Zhao *et al.* 2010). Mycosubtilin overproduced by *B. subtilis* strain BBG100 significantly reduced fungal infection of tomato seedlings caused by *Pythium aphanidermatum*, while overproduction of the same iturin by *B. subtilis* strain BBG125 showed antifungal activity against *B. cinerea* and *F. oxysporum* (Béchet *et al.* 2013; Leclère *et al.* 2005).

The surfactin family consists of amphiphilic cyclic peptides composed of 7 α -amino acids attached to a single β -hydroxy fatty acid of 13 to 16 carbons in length (Jacques, 2011). These biosurfactants are compounds produced by microbial cells, distributed over their surface, or excreted to reduce surface and interfacial tension while contributing to cell motility, adhesion to biofilm formation, and plant immune responses (Costa *et al.* 2018; Fira *et al.* 2018; Jourdan *et al.* 2009). Different variants of surfactin, pumilacidin, lichenisin, and halobacilin belong to this family. In addition to the aforementioned properties, they are also known for their ability to induce irreversible pore and ion channel formation in cell membranes of various bacteria, viruses, and fungi, thereby disrupting and destabilizing them (Ongena & Jacques, 2008). The mechanism of membrane disruption begins with surfactants binding to the outer membrane of the bacterial cell envelope and penetrating the bacterial cell wall before interacting with the inner phospholipid membrane. It has been found that size, charge, molecular architecture, critical micellar concentration, aggregation numbers, chain length, and degree

of saturation are all properties of surfactants that strongly influence their binding efficacy. On the other hand, whether surfactants dissolve the outer membrane or penetrate the phospholipid structure of the inner membrane through channels remains an open question (Sharma *et al.* 2022). Once they reach the membrane, dimerized surfactins insert into lipid bilayers, helate mono- and divalent cations, and alter cell membrane permeability either through channel formation or detergent-like membrane solubilization (Fracchia *et al.* 2012; Sharma *et al.* 2022). Surfactins, especially surfactin and pumilacidin, produced by various strains of *B. subtilis*, *B. amyloliquefaciens* and other *Bacillus* species showed considerable antimicrobial activity against many plant pathogens, such as *S. sclerotiorum*, *R. solani*, *Fusarium solani*, *X. axonopodis* pv. *glycines*, *Aspergillus flavus*, *C. gloeosporioides*, *P. aphanidermatum*, *S. rolfsii*, *M. grisea*, *Curvularia lunata*, *Rhizoctonia bataticola* and *Fusarium verticillioides* (Li *et al.* 2014; Melo *et al.* 2009; Mohammadipour *et al.* 2009; Preecha *et al.* 2010; Snook *et al.* 2009; Tendulkar *et al.* 2007). In one of the previous studies, mass spectrometry analysis confirmed the presence of surfactin in the ethyl acetate extract of *B. amyloliquefaciens* strain SS-12.6, which showed strong growth inhibitory properties against a wide range of postharvest fungal pathogens, *in vitro* and *in situ*, on apple fruit as well as against all tested strains of *X. arboricola* pv. *juglandis* from walnut fruit (Dimkić *et al.* 2013).

Lipopeptides from the fengycin family are amphiphilic cyclic peptides composed of 10 α -amino acids attached to a β -hydroxy fatty acid of 14 to 18 carbons in length (Jacques, 2011). These compounds were extracted mainly from *B. subtilis* and also act on the target cells by interacting with the cell membrane and changing its structure and permeability (Deleu *et al.* 2008; Fira *et al.* 2018). Fengycins, highly recognized for their antimicrobial properties, have been the subject of numerous studies demonstrating their growth inhibitory activities against fungi such as *F. oxysporum*, *Fusarium graminearum*, *Fusarium culmorum*, *Fusarium moniliforme*, *Mycosphaerella fijiensis*, *B. cinerea*, *M. laxa/fructicola*, *R. solani*, *Verticillium dahliae*, *F. solani*, *Phytophthora parasitica*, and *C. gloeosporioides* (Chan *et al.* 2009; Falardeau *et al.* 2013; Rebib *et al.* 2012; Villegas-Escobar *et al.* 2013; Yáñez-Mendizábal *et al.* 2012).

Kurstakins are lipopeptides produced primarily by *Bacillus thuringiensis* but also found in other species of the genus *Bacillus*, such as *B. cereus*. It has been discovered that their antimicrobial activity is also due to their ability to form pores in cell membranes, but their activity is recognized as species-specific. *Stachybotrys chartarum* is one of the fungi

sensitive to kurstakins produced by *B. thuringiensis* (Béchet *et al.* 2012). Many studies have shown that different lipopeptide antimicrobial compounds often cooperate with the common goal of suppressing the activity of phytopathogens. For example, antifungal activity against the fungus *Pestalotiopsis eugeniae* was activated when both iturin A and surfactin produced by *B. subtilis* BS-99 were present (Lin *et al.* 2011). Moreover, the cooperation between lipopeptides did not prove to be a unique case, as compounds produced by antagonistic *Bacillus* strains in synergy with savory oil or when thyme and savory oils were applied simultaneously *in situ* to marigold seeds, also showed positive effects on reducing overall fungal infection without adverse effects on seed germination (Dimkić *et al.* 2015).

Bacillus species can act via the induction of systemic resistance in plant hosts by producing various volatiles, such as alcohols, aldehydes, aromatics, sulfides and ketones. By activating jasmonic acid, salicylic acid or ethylene signaling pathways, compounds from *Bacillus* species (e.g., lipopeptides, polyketides, and volatiles) stimulate the expression of genes encoding pathogenesis-related proteins and other defense-related proteins in plant hosts. These compounds have also been shown to be able to inhibit quorum sensing in competing bacteria as well as inhibit the expression of genes involved in mycelial growth, penetration, sporulation, and virulence of fungal pathogens (Dimkić *et al.* 2022).

4. Conclusions

In view of the studies mentioned so far, the metabolites of *Pseudomonas* spp. and *Bacillus* spp. have immense biological control potential against a wide range of agronomically important fungal and bacterial phytopathogens. Thus, instead of applying already overproduced chemical fertilizers and pesticides, the use of *Pseudomonas* and *Bacillus* strains in the form of bioformulations can achieve the same, if not better, results in protecting plant health while maintaining ecosystem health. At the same time, lower production costs make BCAs much more affordable for many farmers in developing countries, which is another step toward sustainable agriculture.

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