REVIEW ARTICLE

Exploiting Bacterial Genera as Biocontrol Agents: Mechanisms, Interactions and Applications in Sustainable Agriculture

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Abstract
The rising demand for sustainable agriculture necessitates alternative methods to using chemical pesticides for controlling plant pathogens. Biocontrol involves the use of natural antagonists, such as bacteria, as an alternative to synthetic chemical pesticides, which can be harmful to human health and the environment. This review discusses the potential of *Bacillus*, *Streptomyces*, *Pseudomonas* and *Serratia* as biocontrol agents (BCAs) against various plant pathogens. These bacteria suppress pathogen growth via various mechanisms, such as antibiosis, nutrient and space competition and systemic resistance, and significantly contribute to plant growth. We provide an overview of the secondary metabolites, plant interactions and microbiota interactions of these bacteria. BCAs offer a promising and sustainable solution to plant pathogens and help maintain the one-health principle.

Keywords Plant–microbe interaction · Biocontrol · Sustainable agriculture · *Bacillus* · *Streptomyces* · *Pseudomonas* · *Serratia*

Background

The use of natural antagonists, such as bacteria, as biocontrol agents (BCAs) has gained considerable attention in recent years as a sustainable approach to managing pests, pathogens and diseases in agriculture. *Bacillus*, *Streptomycetes*, *Pseudomonas* and *Serratia* species are key players in biocontrol. Given the rising demand for sustainable agriculture, this review discusses the potential of these bacteria as BCAs against various plant pathogens.

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Bacillus

Bacillus are gram-positive rod-shaped bacteria which can either be aerobes or anaerobes (Turnbull 1996). As BCAs, specifically plant growth-promoting rhizobacteria, *Bacillus* protect plants through antibiosis, signal interference, induced systemic resistance and niche competition (Todorova and Kozhuharova 2010; Blake et al. 2021). Furthermore, *Bacillus* improve nutrient availability, alter plant growth hormone homeostasis and reduce abiotic stress to promote growth, offering an advantage for commercial use (Blake et al. 2021).

Interactions with Plants

Biocontrol Mechanisms

Bacillus are one of the most widely researched rhizobacteria and highly promising option for agricultural uses. They possess various direct and indirect mechanisms against phytopathogens. The main biocontrol secondary metabolites produced by *Bacillus* and their corresponding functions are outlined in Fig. 1 and Table 1.
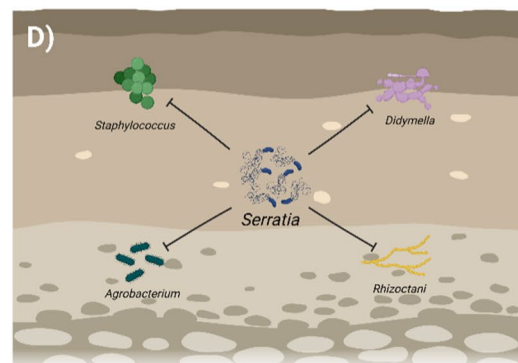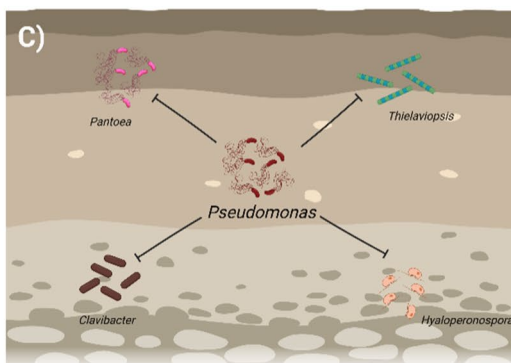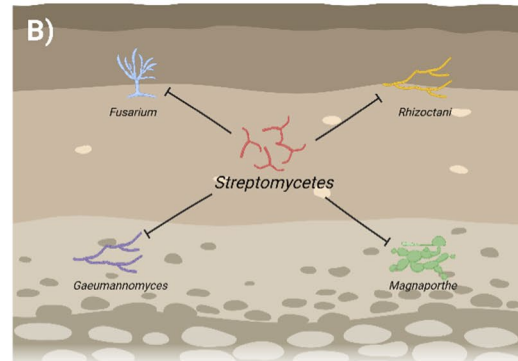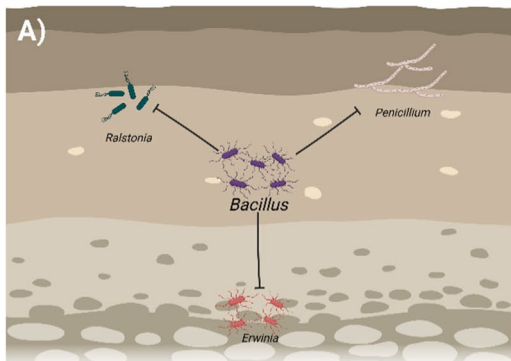
Induced Systemic Resistance

Aside from direct inhibition of pathogens, *Bacillus* enhances

plant defences through induced systemic resistance (ISR). When beneficial bacteria are inoculated in the roots, the

◀**Fig. 1** Multifaceted roles of biocontrol agents and their metabolites in enhancing plant immunity and growth. BCAs secrete metabolites that directly or indirectly boost plant immunity. Metabolites such as chitinase and HCN can directly attack plant pathogens. Many VOCs can inhibit pathogen growth or enhance plant immunity. Some metabolites, such as acetoin, can enhance plant growth. **A** *Bacillus* can inhibit plant pathogens, such as *Ralstonia, Penicillium* and *Erwinia*. *Bacillus amyloliquefaciens* (BA) secretes volatile organic compounds (VOCs) to inhibit *Penicillium digitatum* and *Ralstonia solanacearum*. *B. subtilis* BS-1 produces AiiA, which can decrease the symptoms of disease caused by *Erwinia carotovora*. **B** Streptomycetes can inhibit plant pathogens, such as *Fusarium, Rhizoctani, Gaeumannomyces*, and *Magnaporthe*. *Streptomyces lydicus* WYEC108 produces chitinase to lyse the cell wall of fungi, such as *Pythium*. **C** *Pseudomonas* can inhibit plant pathogens, such as *Pantoea, Thielaviopsis, Clavibacter* and *Hyaloperonospora*. *Pseudomonas protegens* Pf-5 secretes pyoluteorin, which can reduce the growth of *Pantoea ananatis* DZ-12. *Brassicacearum* LBUM300 uses HCN against *Clavibacter michiganensis* and *Thielaviopsis basicola*. **D** *Serratia* can inhibit plant pathogens, including *Staphylococcus, Didymella, Agrobacterium* and *Rhizoctani*. Prodigiosin, produced by *Serratia*, has antagonistic effects on methicillin-resistant *Staphylococcus aureus* (MRSA), *Staphylococcus epidermidis, Staphylococcus saprophyticus, Streptococcus pyogenes, Enterobacter faecalis, Bacillus cereus, Acinetobacter anitratus, Agrobacterium tumefaciens* and *Bacillus licheniform* (ORSA). *Serratia marcescens* produces Serrawettin W2, which has anti-bacterial activity against *Staphylococcus aureus*

defence capacity of the entire plant against various pathogens is enhanced (Kloepper et al. 2004).

B. subtilis generates many compounds which can elicit ISR. Tomato and bean leaves with high levels of surfactin- and fengycin-producing *B. subtilis* in their roots are more resistant to diseases caused by *Botrytis cinerea* than those without *B. subtilis* (Ongena et al. 2007). For instance, BA strain S13-3 triggers plant defence in strawberry leaves by generating iturin A and surfactins (Yamamoto et al. 2015a). The absence of *B. subtilis* in the leaves shows that disease reduction is via ISR (Yamamoto et al. 2015b). Furthermore, BA strains can trigger ISR by producing VOCs such as 2,3-butadial and 3-hydroxy-2butanone(acetoin) and stimulating defence enzymes (Farag et al. 2013).

Plant Growth Promotion

Bacillus promotes plant growth via diverse mechanisms, such as providing important plant trace elements and nutrients. Nitrogen, which is an inaccessible form in the natural environment, must be mobilised into an accessible form like nitrate or ammonium ions before being used (Hayat et al. 2010). *B. subtilis* can fix unavailable atmospheric nitrogen to a usable form for plants. It also helps nodulation by other bacteria, leading to the colonisation of native symbiotic rhizobacteria (Elkoca et al. 2007).

Bacillus not only improves nutrient availability but also alters plant growth hormone homeostasis to promote plant growth. It can promote plant growth and cell division by producing growth hormones themselves or by inducing plant production via secreted compounds (Arkhipova et al. 2005). Acetoin (3-hydroxy-2-butanone) and 2,3-butanediol are VOCs produced by *B. subtilis* that can affect cytokinin and ethylene homeostasis. The leaf size of *Arabidopsis thaliana* significantly increases when inoculated with *B. subtilis* and pure 2,3-butanediol but not when inoculated with mutants of the cytokinin and ethylene pathways (Ryu et al. 2003). Furthermore, BA contains the genes *patB, dhaS, yclB, yclC, yhcX* and *ysnE*, which are implicated in indole-3-acetic acid (IAA) production. IAA can control several plant growth processes, including elongation, cell division, fruit development and root hair production stimulation (Baard et al. 2023; Schulten and Schnitzer 1997; Chen et al. 2017). IAA can also boost the quantity and length of main and lateral roots, increasing plant water and nutrient absorption (Beyeler et al. 1999; Zhang et al. 2014; Wang et al. 2023a).

Bacillus can also indirectly promote plant growth by reducing abiotic stresses. Two major restrictions for modern agriculture, water and salt stresses can be reduced by *Bacillus* (Li et al. 2009; Woo et al. 2020). Inoculating *B. subtilis* GOT9 in *A. thaliana* and *Brassica campestris* enhances tolerance to drought and salt stresses. It regulates the expression of plant genes such as phosphoethanolamine N-methyltransferase (PEAMT), especially those associated with abscisic acid, which is a key hormone for regulating stress in plants (Zhang et al. 2010). The main metabolites produced by *Bacillus*, which promote plant growth, and their corresponding functions are outlined in Fig. 1 and Table 2.

Interactions with the Microbiota

Antibiosis

Bacillus produce different anti-microbial compounds, including lipopeptides, exoenzymes and volatile organic compounds (VOCs) (Wang et al. 2015).

Lipopeptides, such as surfactin, protect plants against pathogens (Sansinenea and Ortiz 2011). Given its amphiphilicity, surfactin disrupts the cell membranes of other organisms by integrating into the lipid layers and, thus, reducing surface tension (Ongena and Jacques 2008). The survival rate of *Arabidopsis thaliana* remarkably increases when infected with *Pseudomonas syringae* and inoculated with surfactin-producing *Bacillus subtilis* but not when inoculated with a surfactin mutant strain (Putri et al. 2023). Fan et al. (2017) found that *B. subtilis* 9407, a surfactin producer, exerts strong anti-bacterial activity against *Acidovorax citrulli* and efficient biocontrol on melon seedlings in controlled greenhouse tests.

Bacillus produce exoenzymes, such as proteases and chitinases, which can decompose the fungal cell wall (Blake et al. 2021). Chitinase is one of the main anti-fungal components produced by *Bacillus*. Greenhouse and field test results

Table 1 Secondary metabolites produced by biocontrol agents with biocontrol activity

Category	Metabolites	Function	Bacteria species
Lipopeptide	Surfactin	Antibiosis, ISR	*Bacillus*
	Bacillomycin D	Antibiosis	*Bacillus*
	Fengycin	ISR	*Bacillus*
	Iturin A	ISR	*Bacillus*
	Sessilin	Antibiosis	*Pseudomonas*
Exoenzyme	Protease	Antibiosis	*Bacillus*
	Chitinase	Antibiosis	*Bacillus, Streptomyces*
	AiiA	Signal Interference	*Bacillus*
	Phenylalanine ammonia-lyase	ISR	*Bacillus*
	Peroxidase	ISR	*Bacillus*
VOCs	Dimethyl Disulfide	Antibiosis	*Serratia*
Macrocyclic Lactone	Avermectin	Antibiosis	*Streptomyces*
Tripyrrole pigments	Prodigiosin	Antibiosis	*Serratia*
Beta-lactam antibiotics	carbapenem group(1-carbapen-2-em-3-carboxylic acid)	Antibiosis	*Serratia*
Biosurfactants	serrawettins	Antibiosis	*Serratia*
Thiopeptide antibiotics	Althiomycin	Antibiosis	*Serratia*
Polyketide-type natural product	Oocydin A	Antibiosis	*Serratia*
	DAPG	Antibiosis, ISR	*Pseudomonas*
Tricyclic compounds with nitrogen	Phenazine	Antibiosis, ISR	*Pseudomonas*
Etc	Pyoluteorin	Antibiosis	*Pseudomonas*
	HCN	Antibiosis	*Pseudomonas*
	Rhizoxin	Antibiosis	*Pseudomonas*
	Promysalin	Antibiosis	*Pseudomonas*
	I-furanomycin	Antibiosis	*Pseudomonas*
	Fit toxin	Antibiosis	*Pseudomonas*
	Siderophore	ISR	*Pseudomonas*

Exoenzyme: AiiA: AHL lactonase, VOCs: volatile organic compounds, polyketide-type natural product: DAPG: 2,4-diacetylphloroglucinol, ETC: HCN: hydrogen cyanide, ISR: induced systemic resistance

Table 2 Secondary metabolites produced by biocontrol agents with plant growth promotion ability

Category	Metabolites	Bacteria species
VOCs	Acetoin	*Bacillus*
	2,3-butanediol	*Bacillus*
Phytohormone	IAA	*Bacillus*
Polyketide-type natural product	DAPG	*Pseudomonas*

VOCs: volatile organic compounds, phytohormone: IAA: indole acetic acid, polyketide-type natural product: DAPG: 2,4-diacetylphloroglucinol

showed that inoculating plants with chitinase-producing *B. subtilis* strain significantly reduces the incidence of diseases by 20–35% (Yan et al. 2011).

Bacillus also produce volatiles which can inhibit the spore germination and hyphal growth of phytopathogens in a contact-independent manner on agar plates (Grahovac et al. 2023). *Bacillus amyloliquefaciens* (BA) strains produce anti-microbial VOCs (Luo et al. 2022). For example, BA strains JBC36, SQR-9 and T-5 produce VOCs such as pentadecane, ethyl benzene and benzothiazole, which can inhibit *Penicillium digitatum* and *Ralstonia solanacearum* growth (Yu et al. 2012; Raza et al. 2016).

Signal Interference

Bacillus can also reduce disease intensity by reducing pathogen virulence (Pan et al. 2008). Interfering with quorum sensing (QS) signals could be an effective strategy to prevent diseases (Helman and Chernin 2015). *B. subtilis* produces AiiA, an enzyme which inactivates QS autoinducers (Pan et al. 2008; Dong et al. 2000; Lyng and Kovács 2023). *B. subtilis* BS-1, which produces AiiA, can decrease symptoms of potato soft rot caused by *Erwinia carotovora*, a pathogen dependent on autoinducers for virulence (Pan et al. 2008).

The rhizosphere harbours up to 10^{11} microbial cells per gram, representing more than 30,000 species (Berendsen et al. 2012). Most studies have been conducted in highly controlled conditions, which complicate replicating their results in natural environments. One of the crucial reasons for natural field variabilities is plant microbiomes. Numerous variables affect the microbial communities found in soil and around roots; consequently, these variables may also affect the efficacy of biocontrol methods (Rousk et al. 2010; Pershina et al. 2018). These elements can be broadly classified into two types. First, abiotic factors can affect microbial assemblages, including soil type (which is determined by properties such as water content, nutrient levels, pH and trace metals), climate and farming practices, such as fertilisation, tillage, irrigation and pre-cropping (Rousk et al. 2010; Pershina et al. 2018). Second, biotic parameters include host genetics, host crop species, root exude characteristics, plant age at application and competing microbes already present in the plant microbiome (Haichar et al. 2008; Turner et al. 2013; Bressan et al. 2009; Micallef et al. 2009; Chaparro et al. 2014; Edwards et al. 2018; Bakker et al. 2015). Interactions between microbes, whether cooperative or competitive, can either enhance or impede the colonisation of *Bacillus* on roots or even determine its success (Blake et al. 2021).

Bacillus to be used as BCAs should adapt to natural ecology and preserve the original microorganisms. Indeed, adding *Bacillus* to a natural rhizosphere has minimal impact on the natural rhizosphere bacterial community. A previous study inoculated *B. subtilis* PTS-394 into tomatoes; results showed that the bacterial community 1 day after inoculation is distinct from that in the control, but the bacterial community 14 days after inoculation is similar to that in the control (Qiao et al. 2017). This result indicates that *Bacillus* do not spoil the natural existing plant microbiome. However, the effects of the natural plant microbiome on *Bacillus* warrant further investigation.

Streptomycetes

Streptomycetes, a gram-positive genus belonging to Actinobacteria, has drawn considerable attention owing to its potential as a sustainable BCA (Pacios-Michelena et al. 2021). *Streptomyces* species in plant root microbiomes produce inhibiting metabolites against pests and pathogens.

Interactions with Plants

Biocontrol Mechanisms

Streptomyces are soil bacteria which serve as BCAs via several ways. They produce anti-microbials, enzymes, VOCs and anthelmintic compounds. They also indirectly inhibit phytopathogens (Newitt et al. 2019a). The main biocontrol secondary metabolites produced by *Streptomyces* and their corresponding functions are outlined in Fig. 1 and Table 1.

Induced Systemic Resistance

Streptomyces can indirectly suppress plant pathogens through competitive exclusion and activation of host resistance mechanisms (Ebrahimi-Zarandi et al. 2022). ISR promotes various changes, including the accumulation of defence-related chemicals, localised cell death and cell wall reinforcements, resulting in an enhanced and more efficient response to future pathogenic onslaught (Viaene et al. 2016; Lugtenberg and Kamilova 2009; Kurth et al. 2014). Inoculating oak trees with *Streptomyces* sp. AcH505 upregulates the expression of pathogenesis-related proteins (Kurth et al. 2014).

Plant Growth Promotion

When searching for novel BCAs, *Streptomyces* are becoming a more visionary choice because of their capacity to colonise plant roots and ability to create strong anti-microbial secondary metabolites (Díaz-Díaz et al. 2023). This is especially true given that members of this genus promote plant growth under normal and stressful environmental conditions, such as high salinity, and protect plants from diseases (Viaene et al. 2016; Chater 2006; Palaniyandi et al. 2014; Tripathi and Singh 2018). These additional advantages may serve as the basis for highly desirable BCAs which can promote plant growth and protect against diseases (Newitt et al. 2019a).

Interactions with the Microbiota

Disease-Suppressive Soil

Streptomyces can directly protect plant hosts against infections in the soil, rhizosphere and endosphere by producing anti-microbial chemicals or particular enzymes, including cellulases, chitinases and proteases (Meij et al. 2017). Disease-suppressive soils are well-known examples of microbial-based protection against soil-borne pathogens (Weller et al. 2002). *Streptomyces* species are enriched in these soils and strains have been utilised to create the biofungicide Mycostop®, which is effective against diverse crop diseases, including wheat head blight caused by *Fusarium* (Lahdenperä et al. 1991).

Antibiosis

In addition to disease-suppressive soils, *Streptomyces* can act as BCAs by producing anti-microbials, exoenzymes, VOCs and anthelmintic compounds (Newitt et al. 2019b).

Streptomyces can inhibit *Magnaporthe oryzae*, *Gaeumannomyces graminis* var. *tritici*, *Fusarium* species and *Rhizoctani solani* in vitro (Dean et al. 2012; Law et al. 2017). Administration of *Streptomyces* BN1 (isolated from *Fusarium*-contaminated rice grains) to seeds as a spore preparation ameliorates the reduction in seedling length caused by *Fusarium* (Jung et al. 2013). *Streptomyces* are promising BCAs for take-all wheat disease because of its saprotrophic and spore-forming lifestyle, which allows it to persist under harsh environments (Meij et al. 2017; Coombs et al. 2004).

Streptomyces encode a huge number of secreted proteins with a wide range of extracellular functions; for instance, they can produce chitinases, which breakdown chitin (Wang et al. 2023b). Chitinases are gaining popularity as BCAs because of their capacity to suppress a wide range of phytopathogenic fungi and oomycetes (Chater et al. 2010). Purified chitinase from *Streptomyces lydicus* WYEC108 can lyse the cell walls of numerous phytopathogenic fungi, including *Pythium*, which may cause root rot in cereal crops (Mahadevan and Crawford 1997).

Streptomyces is a prolific generator of VOCs, which are small molecules with low weights and high vapour pressures (Mendes et al. 2013; Cordovez et al. 1081; Wheatley 2002). Several VOCs exert anti-bacterial activities against phytopathogenic organisms, such as *R. solani* (Mendes et al. 2013; Chapelle et al. 2016). These compounds may be utilised as biofumigants to restrict the growth of pathogenic organisms and prevent soil-borne diseases (Newitt et al. 2019a). Some studies suggested the use of VOCs as biofumigants (Gong et al. 2022). However, further research is necessary to confirm whether these chemicals are synthesised in vivo in the plant root system and effective under natural settings (Newitt et al. 2019a).

Streptomyces generate effective anthelmintic chemicals, such as avermectin, which may kill cereal cyst nematodes (Burg et al. 1979; Huang et al. 2014). Some *Streptomyces* species can regulate nematode populations (Nour et al. 2003; Samac and Kinkel 2001; Zhang et al. 2020).

The antagonistic behaviour of strains which prevent the establishment of plant pathogenic microbes in soil can exclude beneficial species and disturb important biogeochemical cycles, among other unintended consequences (Chaparro et al. 2014). Some *Streptomycetes* species produce antibiotics and prevent the formation of nodules by nitrogen-fixing bacterial species in the roots of leguminous plants and the beginning of plant host symbioses with mycorrhizal fungus (Gregor et al. 2003; Samac et al. 2003; Schrey and Tarkka 2008). However, other *Streptomyces* species can promote mycorrhizal development and nodulation while inhibiting pathogenic growth. Therefore, candidate biocontrol species must be selected and screened carefully (Gregor et al. 2003).

Pseudomonas

Pseudomonas is a genus of the *Gammaproteobacteria* (Battistuzzi and Hedges 2009). Some of their characteristics are useful in plant growth promotion and biocontrol (Peix et al. 2009). Many *Pseudomonas* strains can directly stimulate plant development in no pathogen condition by enhancing mineral nutrient availability and uptake through phosphate solubilisation. Moreover, they can enhance root growth by synthesising phytohormones or increasing tolerance to abiotic stress. They are effective soil-borne disease controllers and good root colonisers. Certain *Pseudomonas* strains can also prevent leaf diseases through ISR in plants. Typically, *Pseudomonas* biocontrol strains do not survive well on above-ground plant parts, with the exception of a few strains from *P. syringae*.

Interactions with Plants

Biocontrol Mechanisms

Pseudomonas have several mechanisms that can suppress plant disease. They can secrete antibiosis, compete with other bacteria for nutrients or space, and trigger ISR. Particularly, secondary metabolites of *Pseudomonas* are key players in the biocontrol of plant diseases. The main biocontrol secondary metabolites produced by *Pseudomonas* and their corresponding functions are outlined in Fig. 1 and Table 1.

Induced Systemic Resistance

Some secondary metabolites mentioned earlier can trigger ISR. In many plants, phenazines cause ISR (Ma et al. 2016). DAPG can trigger ISR in Arabidopsis by inducing jasmonate- and ethylene-mediated defence responses to the mildew pathogens *Hyaloperonospora parasitica*, *Pseudomonas syringae* pv. tomato and *Botrytis cinerea* (Iavicoli et al. 2003; Weller et al. 2012; Chae et al. 2020). Siderophores, along with other bacterial secretions, can trigger ISR in plants. Specifically, *Pseudomonas aeruginosa* 7NSK2 produces the siderophores pyoverdine and pyochelin. These compounds have demonstrated effectiveness in protecting plants from diseases caused by pathogens such as *Pythium splendens* and *Botrytis cinerea* (Aznar and Dellagi 2015). In addition, this bacterium secretes pyocyanin, a phenazine compound. Notably, it has been found that pyocyanin, in conjunction with pyochelin, can induce ISR, thereby protecting tomatoes against diseases caused by *B. cinerea* through the promotion of ROS accumulation (Audenaert et al. 2002).

Plant Growth Promotion

Pseudomonas strains can promote plant growth through several mechanisms. DAPG interferes with the auxin-dependent signalling system and promotes root branching in tomatoes, and it can stimulate amino acid exudation from plant roots (Phillips et al. 2004; Brazelton et al. 2008). Biosurfactants are secondary metabolites involved in root growth, nutrient availability, swarming movement, biofilm formation, environmental adaptation and nutrient cycling (D'Aes et al. 2010; Oni et al. 2015; Raaijmakers et al. 2010). The main metabolites produced by *Pseudomonas*, which promote plant growth, and their corresponding functions are outlined in Fig. 1 and Table 2.

Interactions with the Microbiota

Pseudomonas strains are commonly found in natural environments, particularly soil. *P. chlororaphis* isolates have been found from the soil and rhizosphere of crops, such as potato, tomato, radish, beet, maize, soja, alfalfa, sugarcane and clover (Biessy et al. 2019). Rhizopus and brown rot diseases on peaches can be successfully suppressed by *P. syringae* isolates MA-4 and NSA-6 from the phyllosphere of apples in Canada (Yang and Hong 2020). *P. protegens 1B1*, *P. clororaphis 48G9* and *P. brassicacearum 93G8* can reduce the incidence of hairy root disease caused by *Agrobacterium rhizogens* by up to 95% on Kalanchoe, soybean and tomato (Freitas and Taylor 2023).

In addition, *Pseudomonas* can form synergistic relationships with other species. In the cucumber rhizosphere, syntrophic cooperation between *Bacillus velezensis* SQR-9 and *Pseudomonas stutzeri* is highly dependent on the environment and involves pathways for the biosynthesis of branched-chain amino acids. The relationship, which promotes plant growth and reduces salt stress, is dependent on *Bacillus* biofilm matrix components (Sun et al. 2022).

Several studies have investigated the impact of *Pseudomonas* strains on non-target organisms, particularly microbial species and total microbial populations. Wild-type and genetically modified DAPG-overproducing *Pseudomonas* BCAs do not interfere with arbuscular mycorrhizal fungi symbiosis, which establish symbiotic partnerships with the majority of land plants (Barea et al. 1998; Edwards et al. 1998; Vázquez et al. 2000). The effect of the native culturable bacterial and fungal populations on the cucumber rhizosphere has been studied using the wild-type *P. fluorescens* strain CHA0-Rif and a derivative CHA0-Rif/pME3424 which overproduces DAPG and pyoluteorin. Some researchers found no changes in the frequency of dominant bacterial groups (Natsch et al. 1998). Others noted a discernible impact on the population of culturable fungi, but it was smaller than the results of consistently producing cucumbers in the same soil (Girlanda et al. 2001).

Antibiosis

Secondary metabolites from *Pseudomonas* can exert antimicrobial and insecticidal activities. In most cases, a single type of secondary metabolite exhibits pleiotropic effects. One of the most conserved metabolites is phenazines. *Pseudomonas* produce phenazines, which are tricyclic compounds that contain nitrogen and are redox-active (Mavrodi et al. 2006). Biocontrol strains mainly generate 2-hydroxyphenazine (1-OH-PHZ, brick-red) or 2-hydroxyphenazine-1-carboxylic acid (PCA, citrus yellow) (2-OH-PCA, orange). The production of phenazines in *Pseudomonas* is regulated by QS, which involves the GacS/GacA two-component signal transduction system. Phenazines have a broad-spectrum action against bacterial, fungal and oomycete diseases, including those caused by *Rhizoctonia solani*, *Streptomyces scabies* and *Phytophthora infestans* (Thomashow and Weller 1988; Jaaffar et al. 2017; Arseneault et al. 2015; Morrison et al. 2017).

Another well-conserved metabolite among *Pseudomonas* strains is 2,4-diacetylphloroglucinol (DAPG). This polyketide antibiotic is predominantly synthesised by *P. protegens* and *P. corrugata*, along with a limited number of strains from other taxonomic families (Almario et al. 2017). DAPG is effective against bacteria, nematodes, oomycetes and fungi, making it crucial in the biocontrol of diseases in the roots and seedlings. *Pseudomonas* sp. LBUM300 produces DAPG, which exhibits antagonistic activity against *Clavibacter michiganensis* subsp. *michiganensis* in vitro and in planta (Lanteigne et al. 2012).

Pseudomonas strains, particularly *P. protegens* and a few *P. aeruginosa* isolates, produce pyoluteorin (Ramette et al. 2011; Hu et al. 2005). In *Pantoea ananatis* DZ-12, which causes maize brown rot on leaves, *P. protegens* Pf-5 exhibits biocontrol activity and extracts a crude extract that includes pyoluteorin. Pyoluteorin significantly prevents DZ-12 growth and causes cytoplasmic extravasations and cell hollowing (Gu et al. 2022).

Hydrogen cyanide (HCN) produced by *Pseudomonas* exhibits multifaceted effects on pathogens owing to its cellular function. The respiratory toxin HCN prevents many species from producing cytochrome c oxidase, which is the final link in the respiratory chain. *P. aeruginosa* and different subsets of *P. fluorescens* contain recognised HCN producers. In *Pseudomonas*, HCN production is often associated with DAPG synthesis, particularly in the *P. corrugate*, *P. protegens* and *P. chlororaphis* subgroups. Tobacco black root rot induced by *Thielaviopsis basicola* is prevented by HCN produced by *P. protegens* CHA0 (Voisard et al. 1989). Additionally, *Pseudomonas*-produced HCN suppresses root-knot

nematodes, aphids, termites and other insects (Siddiqui et al. 2006; Kang et al. 2019; Devi and Kothamasi 2009; Flury et al. 2017).

Few *Pseudomonas* bacteria can generate various strain-specific bioactive compounds. Rhizoxins, which are generated by a few isolates of *P. protegens* and *P. chlororaphis* MA342, are active against oomycetes and fungi (Ligon et al. 2000). The biocontrol species *Pseudomonas* sp. CMR12a is the only one that produces the anti-microbial cyclic lipopeptide sessilin (D'Aes et al. 2014). *Pseudomonas putida* RW10S1 produces the anti-bacterial promysalin, which attacks gram-positive and gram-negative bacteria (Li et al. 2011; Kaduskar et al. 2017). *P. fluorescens* SBW25 secretes the non-proteinogenic amino acid l-furanomycin, which suppresses gram-negative plant pathogenic bacteria (Trippe et al. 2013).

Serratia

Serratia marcescens, the type species for the newly discovered genus, was first reported in 1823 (Bizio 1823). *Serratia* are gram-negative bacteria from the Enterobacteriaceae family and classified into 18 specie. This group of bacteria includes biologically and ecologically diverse species, ranging from those which are useful to economically beneficial plants to pathogenic species which are harmful to humans. *Serratia* are remarkable for their secondary metabolism and their capacity to create a wide variety of natural bioactive compounds (Kai et al. 2007; Matilla et al. 2015; Domik et al. 2016a).

Interactions with Plants

Biocontrol Mechanisms

Serratia can act as BCAs in plants by competing with other pathogens directly or indirectly. The main biocontrol secondary metabolites produced by *Serratia* and their corresponding functions are outlined in Fig. 1 and Table 1.

Induced Systemic Resistance

Certain Serratia strains, such as *Serratia marcescens* CDP-13, can up-regulate ISR in plants. In water agar tests, wheat plants inoculated with *S. marcescens* CDP-13 exhibited significantly reduced susceptibility to diseases triggered by *Fusarium graminearum* (Singh and Jha 2016). Prior studies support Serratia's ability to enhance ISR, though the specific mechanism of plant disease resistance remains elusive. Therefore, future research should concentrate on the tissue-specific induction of systemic resistance and its correlation

with the reduction of plant pathogen susceptibility (Singh and Jha 2016).

Plant Growth Promotion

Specific Serratia strains are known to promote plant growth. They can produce IAA, which positively influences plant growth, especially when exposed to elevated levels of metalloids such as arsenic (As), cadmium (Cd), chromium (Cr), copper (Cu), manganese (Mn), nickel (Ni), and lead (Pb) (Mondal et al. 2022). Greenhouse experiments demonstrated that plants bacterized with *S. marcescens* NBRI1213 showed significant increases in shoot length, shoot dry weight, root length and root dry weight compared to untreated control plants.

Interactions with the Microbiota

Antibiosis

The unique trait of *Serratia* is the production of prodigiosin (2-methyl-3-pentyl-6-methoxyprodiginine) (Han et al. 2021), a bioactive compound from the prodiginine family. Prodigiosin is a tripyrrole red pigment secreted into the culture medium as a secondary metabolite (Han et al. 2021). Only four species—*S. marcescens, S. plymuthica, S. nematodiphila and S. rubidaea*—can produce prodigiosin (de Murguia 2018). The bacterial plasma membrane is the prodigiosin's primary target (Suryawanshi et al. 2017). As a chaotropic stressor, prodigiosin disrupts the bacterial plasma membrane and causes the loss of vital intracellular components, such carbohydrates, amino acids, proteins and K^+ ions, from cells exposed to it (Suryawanshi et al. 2017). Prodigiosin has broad-spectrum anti-bacterial properties against methicillin-resistant Staphylococcus aureus, Staphylococcus epidermidis, Staphylococcus saprophyticus, Streptococcus pyogenes, Enterobacter faecalis, Bacillus cereus, Acinetobacter anitratus, Agrobacterium tumefaciens and Bacillus licheniform (ORSA) (Nguyen et al. 2022; Yip et al. 2021). Prodigiosin is also effective against other pathogens, including insects, nematodes and phytopathogenic fungi, which affect crops (Choi et al. 2021; Nguyen et al. 2021).

Antibiotics of the carbapenem group are also produced by *Serratia* isolates (Moellering et al. 1989). Carbapenems are a broad group of b-lactam antibiotics characterised by strong anti-bacterial and b-lactamase-inhibitory activity (Moellering et al. 1989). As anti-microbial agents, they have a wide range of uses and are particularly useful in infections caused by bacteria that are resistant to different drugs (Moellering et al. 1989). In *Serratia* sp. And *S. marcescens*, carbapenem production and regulation have been extensively researched (McGowan et al. 1996).

According to Soberon-Chavez and Maier, *Serratia* produces biosurfactants called serrawettins (Soberón-Chávez and Maier 2011). They lack amino acid residues with ionic hydrophilicity, making them non-ionic (Matsuyama et al. 2011). They can alter the hydrophobicity of the cell surface, which is crucial for the adherence of these bacteria to diverse surfaces and helps promote the surface spreading of bacteria in environments with low nutrient availability (Su et al. 2016; Zhang et al. 2021). Serrawettin W1, W2 and W3 are molecular species that have been identified. Serrawettin W1 promotes swarming motility and exhibits a broad-spectrum anti-microbial action, which may help the bacterium survive antibiotics and move into more advantageous microenvironments (Kadouri and Shanks 2013; Lapenda et al. 2015). Serrawettin W2, a biosurfactant which can disperse *Caenorhabditis elegans* and exert anti-bacterial activity against *Staphylococcus aureus*, was initially isolated from *S. marcescens* in 1986 (Pradel et al. 2007). Many *S. marcescens* strains simultaneously generate prodigiosin and serrawettin W1 (Soo et al. 2014). *S. surfactantfaciens YD25* may simultaneously synthesise prodigiosin and serrawettin W2 (Su et al. 2016). In contrast to serrawettins W1 and W2, serrawettin W3 has only been partially characterised (Matsuyama et al. 1986).

Althiomycin is a secondary metabolite of *Serratia*. The non-pigmented model insect pathogen *S. marcescens* strain Db10 produces althiomycin (Gerc et al. 2012). *B. subtilis* grows slowly due to the presence of this diffusible metabolite (Fujimoto et al. 1970).

Anti-fungal

Natural anti-fungal substances have been identified in *Serratia*. Because of its powerful bioactivity against plant pathogenic oomycetes, oocydin A, a chlorinated macrolide, was originally isolated from the plant epiphytic strain *S. marcescens* MSU97 in 1999 (Strobel et al. 1999). Oocydin A is a polyketide-type natural product with anti-fungal activity. *S. plymuthica* strains A153, 4Rx5 and 4Rx13 generate oocydin A (Matilla et al. 2015). The potential of *Serratia* sp. B1_6 to prevent the plant disease caused by *Verticillium dahliae* may be linked to its capacity to produce oocydin A. Several *S. plymuthica* strains exert in vitro anti-fungal activities against fungal infections (Berg 2000). However, the chemical nature of these anti-fungal products remains to be determined.

VOCs

Sodorifen, a recently discovered VOC, is another distinctive substance generated by *S. plymuthica* isolates (Domik et al. 2016b; Weise et al. 2014). Sodorifen, also known as 1,2,4,5,6,7,8- heptamethyl-3-methylenebicyclo[3.2.1] oct-6-ene, is a rare and unique volatile hydrocarbon (Reuß

et al. 2010). The biological function of sodorifen remains unknown, although it may result from terpene metabolism, and the gene cluster in charge of its manufacture has been located (Domik et al. 2016a). *S. plymuthica* PRI-2C produces sodorifen when exposed to VOCs released by the fungus *Fusarium culmorum* (Schmidt et al. 2017). Dimethyl is also a VOC secreted by *Serratia*. *Serratia ureilytica* and *S. bockelmannii* can synthesise dimethyl disulphide in vitro (Abreo et al. 2021). The growth of *Pythium cryptoirregulare* is inhibited by bacterial and exogenous dimethyl disulphide. As a result, *P. cryptoirregulare*-induced damping-off of tomato seedlings is reduced by *S. ureilytica* (Abreo et al. 2021).

The soil is a complex and highly competitive ecosystem, and many soil bacteria react to complex and highly competitive conditions in different ways. Some of these bacteria outcompete other species in their capacity to (1) utilise a wide range of frequently resistant carbon compounds and (2) grow efficiently on those substrates, giving rise to vast populations in a short amount of time (Varivarn et al. 2013). To fight potential competitors, natural soil bacteria frequently use 'chemical warfare', generating and secreting bioactive, inhibiting chemicals (Czaran et al. 2002; Hibbing et al. 2010). Some *Serratia* isolates, particularly those coming from soil, have adopted this strategy (de Murguia 2018). The root and foot rot of *Piper betle* caused by the oomycete *Phytophthora nicotianae* can be biologically controlled by *S. marcescens* NBRI 1213 (Lavania et al. 2006). Wheat fungal infections are reduced by *S. marcescens* CDP-13 (Singh and Jha 2016). *S. plymuthica* HRO-C48 can inhibit the pathogens *V. dahlia* in strawberries, oilseed rapeseed and olive and *Rhizoctonia solani* in lettuce (Kai et al. 2007; Grosch et al. 2005; Kurze et al. 2001). It also produces mVOCs with detrimental effects on the mycelial proliferation of R. *solani* (Kai et al. 2007; Grosch et al. 2005; Kurze et al. 2001). *S. plymuthica* S13 is antagonistic toward *Didymella bryoniae*, the causal agent of black rot in pumpkins under field conditions (Fürnkranz et al. 2012; Muller et al. 2013). *S. plymuthica* 4Rx13 has anti-fungal activities and produces mVOCs, especially sodorifen (Kai et al. 2007; Domik et al. 2016b; Weise et al. 2014). *S. proteamaculans* 1–102 can act as a BCA against *V. dahliae* (Alström 2001).

Concluding Remarks and Future Perspectives

Bacillus, *Streptomycetes*, *Pseudomonas* and *Serratia* show great potential as effective BCAs against various plant pathogens. They use different mechanisms, including antibiosis, competition for nutrients and space, induction of systemic resistance and plant growth promotion, to suppress pathogen growth. However, several improvements, such as optimising

formulation techniques and delivery methods, scaling up production, meeting regulatory requirements and increasing cost-effectiveness, are necessary before they can be successfully implemented in the field. Nevertheless, the use of bacterial BCAs provides a promising and sustainable solution to the plant pathogen problem in agriculture, and their potential applications in promoting plant growth and enhancing soil health make them an important tool in maintaining the one-health principle. Further research and development of these BCAs is essential for the future of sustainable agriculture.

Declarations

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