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Review article

A review on mechanisms and prospects of endophytic bacteria in biocontrol of plant pathogenic fungi and their plant growth-promoting activities

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ABSTRACT

Endophytic bacteria, living inside plants, are competent plant colonizers, capable of enhancing immune responses in plants and establishing a symbiotic relationship with them. Endophytic bacteria are able to control phytopathogenic fungi while exhibiting plant growth-promoting activity. Here, we discussed the mechanisms of phytopathogenic fungi control and plant growth-promoting actions discovered in some major groups of beneficial endophytic bacteria such as *Bacillus*, *Paenibacillus,* and *Pseudomonas*. Most of the studied strains in these genera were isolated from the rhizosphere and soils, and a more extensive study of these endophytic bacteria is needed. It is essential to understand the underlying biocontrol and plant growth-promoting mechanisms and to develop an effective screening approach for selecting potential endophytic bacteria for various applications. We have suggested a screening strategy to identify potentially useful endophytic bacteria based on mechanistic phenomena. The discovery of endophytic bacteria with useful biocontrol and plant growth-promoting characteristics is essential for developing sustainable agriculture.

1. Introduction

It has been estimated that 60 % more food will need to be produced by 2050 to feed the population of more than 10 billion people worldwide [1,2]. The production increase must be maintained despite the loss caused by crop pests and diseases to reach the food demand [2]. The mean global yield losses from crop diseases and pests were approximately 30.3 % in rice, 21.5 % in wheat, 22.6 % in maize, 21.4 % in soybean, and 17.2 % in potato [2]. Plant diseases cause not only significant crop yield losses but also reductions in the

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quality of crops, which impacts human health [3].

Crop plants suffer from various diseases due to infection by phytopathogens. Phytopathogenic fungal infections cause the vast majority of diseases reported in plants. Cereal crops, such as rice, wheat, and maize, are vital sources of human foods, while crops such as tomato, banana, and kiwifruit are key sources of human nutrition. Various fungal pathogens very often colonize these crops. *Magnaporthe oryzae*, the rice blast pathogen, may cause a 10–35 % loss of rice [4]. *Fusarium graminearum* is a devastating fungus that may give rise to head blight, foot rot, and root rot [5] in wheat. This fungus does not only affect yield loss. Still, it may also adulterate wheat grain by producing deoxynivalenol and zearalenone as mycotoxins, which are hazardous to the health of humans and animals [6]. In maize cultivation, fungi are considered critical pathogens, with *Fusarium* spp. being causal agents for infecting roots, stalks, ears, and kernels [7]. In addition to yield loss, *Fusarium* can reduce grain quality by releasing fumonisin or deoxynivalenol [8,9]. *Rhizoctonia solani* may cause diseases in more than 200 species of various plants, including rice, tobacco, and horticultural crops such as tomato, brinjal, potato, pepper, etc. [10]. *Botrytis cinerea* can cause grey mold in various fruits. It can infect multiple fruits, such as grapes, strawberry, raspberry, blackberry, kiwifruit, apple, and pear [11]. It also causes diseases in cabbage, lettuce, broccoli, beans, and carrots [11]. *Sclerotinia sclerotiorum* is a serious cosmopolitan pathogen that causes soft rot or stem rot by infecting a broad range of plants, including sunflower, rapeseed, soybean, lentil, chickpea, peanut, onion, tulip, and various vegetables [12].

Plant disease control primarily depends on chemical pesticide application to manage plant pathogens or vectors of plant pathogens. However, the applications of pesticides may result in hazardous effects on the ecosystem and human lives. So, researchers and producers are searching for eco-friendly disease control techniques. As an alternative tool, plant growth-promoting bacteria (PGPB) can be used to biocontrol plant pathogens [13]. PGPB may inhabit the rhizosphere, episphere, and inside plants [14]. Endophytes inhabit plant tissues without causing disease [15], and some endophytes are also PGPB and thus are considered plant growth-promoting endophytic bacteria (PGPEB) [14].

Endophytes are getting more attention for applications as biocontrol agents and plant growth promoters [16,17]. Endophytic bacteria can be used to control pre- and post-harvest plant pathogens [18]. These bacteria can restrict pathogens by occupying plant tissue space, producing lytic enzymes and secondary metabolites, and developing plant defenses [18,19].

Strains from the bacterial genera of *Bacillus*, *Paenibacillus, Pseudomonas, Burkholderia*, *Enterobacter*, *Klebsiella*, and *Arthrobacter* strains have been reported for their endophytic nature and tested for biocontrol and plant growth-promotion [20–25]. *Bacillus* can produce endospores, thick-walled survival structures allowing microorganisms to bypass stress and adverse environmental situations. These bacteria have a wide spectrum of biocontrol potential, can enhance plant growth, and trigger plant defenses [26,27]. *Paenibacillus* can also produce endospores, live in adverse environments, and assist in controlling plant pathogens through antimicrobial

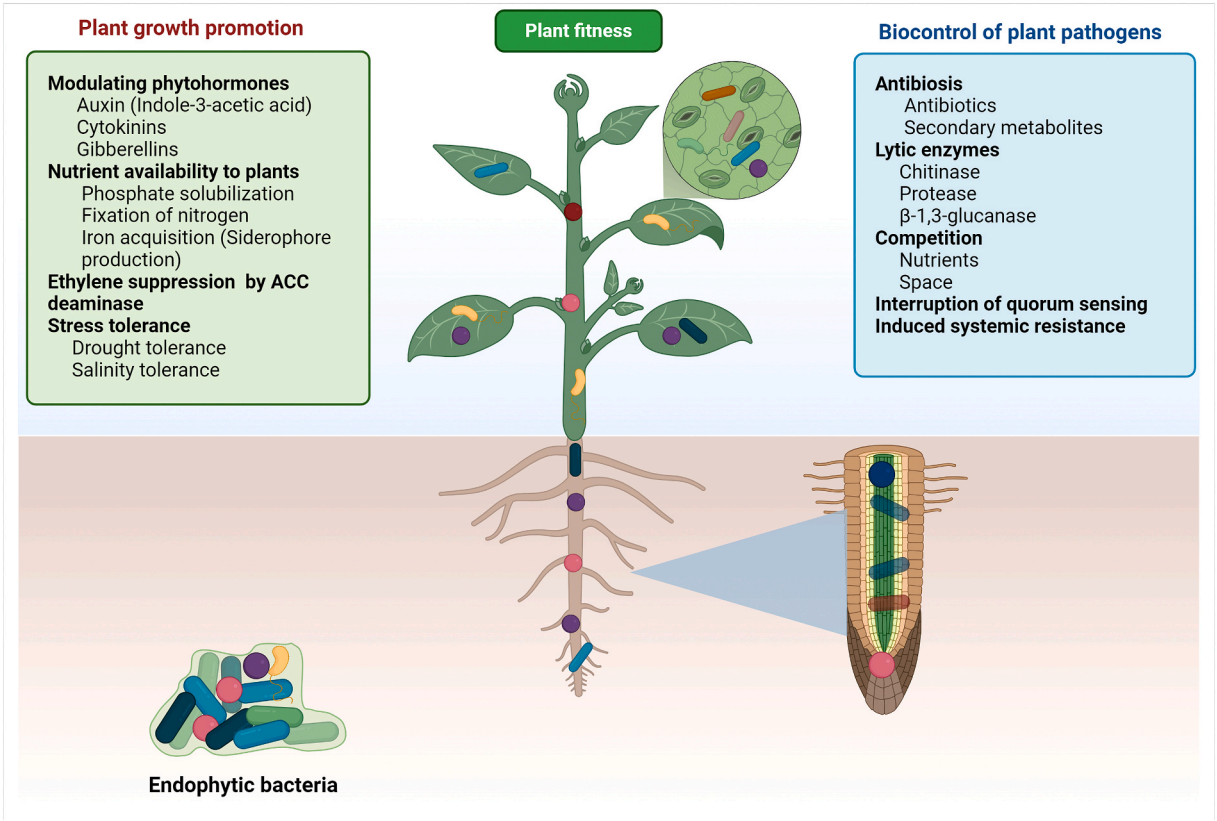


Fig. 1. The schematic representation of endophytic bacterial effects on plant fitness by promoting plant growth and biocontrol of plant pathogens.

production or triggering induced systemic resistance [28]. *Pseudomonas* species are versatile metabolically and can adapt to various environmental conditions. Members of *Pseudomonas* can also restrict phytopathogens and enhance plant growth [22,29].

Recently, many governments around the world have placed various strategies to reduce the usage of agri-chemicals for pest control. In addition, the selection of biocontrol agents and the study of their metabolic and genetic profiles can be extremely important for the scientific community and stakeholders involved in food supply chains. In this review, we discussed the various mechanisms of phytopathogenic fungi control and growth-promoting activity by endophytic bacteria, emphasizing the species belonging to *Bacillus*, *Paenibacillus,* and *Pseudomonas* genera. In addition, we proposed a rapid potential screening approach to identify effective biocontrol and plant-growth-promoting agents.

2. Biocontrol mechanisms of endophytic bacteria

Endophytic bacteria may inhibit plant pathogens as these bacteria can produce various antimicrobial compounds and enzymes to control fungal growth. Endophytic bacteria may also stimulate defense systems through the induction of plant systemic resistance [30,31]. The colonization of useful bacteria and their subsequent competition for nutrients and space can decrease the incidence of plant diseases [18,32]. A list of generalized biocontrol mechanisms is included in Fig. 1. Endophytic bacteria with antifungal and plant growth promotion reported in various studies are presented in Table 1. The biocontrol mechanisms of these bacteria can be described as direct and indirect mechanisms.

2.1. Direct biocontrol mechanisms of endophytic bacteria

2.1.1. Antibiosis

Antibiosis is a process by which bacteria can restrict other microbes by producing antimicrobial compounds. Endophytic bacteria inhibit the growth of phytopathogenic microorganisms by synthesizing secondary metabolites with antifungal and antibacterial activities [47]. Secondary metabolites, including surfactin, iturin, fengycin, bacillaene, subtilosin A, fusaricidin, polymyxin, 2,4-diacetylephloroglucinol (DAPG), phenazine-1-carboxylic acid, 2-hydroxyphenazine, pyrrolnitrine, viscosinamide, and Orfamide are well known for their antimicrobial activity [18,48–52]. For example, *B. subtilis* produces fengycin and inhibits *B. cinerea* in apple fruits [18], *P. fluorescence* produces DAPG and inhibits Thielaviopsis basicola in tobacco [18], and P. polymyxa produces fusaricidins and inhibits Fusarium, Rhizoctonia, Sclerotinia, etc. [52].

2.1.2. Hydrolytic enzymes

Hydrolytic enzymes of endophytic bacteria may break down different polymeric components, including cellulose, chitin, proteins, and lipids [53]. These enzymes can degrade fungal cell walls [18]. The widely reported enzymes for biocontrol include protease, cellulase, β-1,3-glucanase, and chitinase. These enzymes can damage the cell walls of pathogens [54]. For instance, the extra-cellular chitinase of *Pseudomonas aeruginosa* was reported to be able to control *Xanthomonas campestris*, the causal agent of black rot disease in cruciferous crops [55]. The chitinase from *B. subtilis*, when incorporated into a PDA plate, showed a 42.3 % reduction in *R. solani*

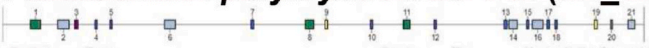
Table 1
List of endophytic bacteria with biocontrol activity.

Strain	Origin	Test fungal pathogens	Inhibition mechanisms	References
Bacillus				
B. subtilis CB2	Wheat seeds	*F. graminearum*	Iturin	[33]
B. subtilis SG_JW.03	Maize seeds	*F. moniliforme*	Fengycin Iturin	[34]
B. amyloliquefaciens YN201732	Tobacco seeds	*Erysiphe cichoracearum*	ISR	[35]
B. velezensis QSE-21	Tomato stem	*B. cinerea*	ISR	[36]
B. velezensis DMW1	Potato tubers	*R. solani* *S. sclerotiorum*	Fengycin Iturin	[37]
B. siamensis WB1	Walnut roots	*C. acutatum*	Fengycin, Iturin	[38]
B. safensis B21	Sweet olive fruits	*M. oryzae*	Iturin	[39]
B. aryabhattai B003	Sweet-grass root	*B. cinerea*	ISR	[40]
Paenibacillus				
P. polymyxa SF05	Maize sheath	*R. solani*	ISR	[41]
P. polymyxa WLY78	Bamboo roots	*F. oxysporum* f. sp. *cucumerium*	Fusaricidins ISR	[42]
P. peoriae RP51	Black locust nodule	*F. graminearum* *R. solani* *M. oryzae*	Fusaricidins	[43]
Paenibacillus sp. UY79	Wild peanut nodule	*B. cinerea* *F. oxysporum* *R. solani*	Fusaricidins	[44]
Pseudomonas				
P. bijieensis XL17	Rape crown gall	*B. cinerea*	DAPG	[45]
P. fluorescens HP72	Bentgrass root	*R. solani*	DAPG	[46]

A. *Bacillus subtilis* NCIB 3610 (NZ_CP094361.1) 14 regions

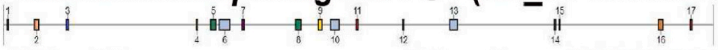
Region	Type	From	To	Most similar known cluster		Similarity
Region 1	ranthipeptide , sactipeptide	203,774	225,847	sporulation killing factor	RiPP:Head-to-tailcyclized peptide	100%
Region 2	NRPS	357,902	421,341	surfactin	NRP:Lipopeptide	82%
Region 3	terpene	1,149,552	1,170,070			
Region 4	transAT-PKS , PKS-like , T3PKS , NRPS	1,763,357	1,868,603	bacillaene	Polyketide+NRP	100%
Region 5	NRPS , betalactone	1,940,219	2,012,961	fengycin	NRP	100%
Region 6	terpene	2,087,392	2,109,290			
Region 7	glycocin	2,254,745	2,274,915	sublancin 168	RiPP:Lanthipeptide	100%
Region 8	T3PKS	2,292,181	2,333,278	1-carbapen-2-em-3-carboxylic acid	Other	16%
Region 9	NRP-metallophore , NRPS	3,255,738	3,307,515	bacillibactin	NRP	100%
Region 10	CDPS	3,588,691	3,609,437	pulcherriminic acid	Other	100%
Region 11	sactipeptide	3,820,955	3,842,566	subtilosin A	RiPP:Thiopeptide	100%
Region 12	other	3,845,565	3,886,983	bacilysin	Other	100%
Region 13	RRE-containing	4,083,044	4,103,313			
Region 14	epipeptide	4,110,636	4,132,334	thailanstatin A	NRP+Polyketide	10%

B. *Paenibacillus polymyxa* ATCC 842 (NZ_CP024795.1) 21 regions



Region	Type	From	To	Most similar known cluster		Similarity
Region 1	NRPS	256,326	350,100	tridecaptin	NRP	100%
Region 2	NRPS , T1PKS , prodigiosin	507,431	613,746	laterocidine	NRP	5%
Region 3	betalactone	664,396	695,274	varlaxin 1046A/varlaxin 1022A	NRP	9%
Region 4	cyclic-lactone-autoinducer	851,259	871,937			
Region 5	cyclic-lactone-autoinducer	989,395	1,009,925			
Region 6	transAT-PKS , NRPS , T3PKS , PKS-like	1,493,208	1,595,143	aurantinin B/aurantinin C/aurantinin D	Polyketide	35%
Region 7	ranthipeptide	2,293,451	2,318,838			
Region 8	NRPS	2,793,810	2,873,397	polymyxin	NRP	100%
Region 9	lanthipeptide-class-i	2,975,546	3,000,094	S-layer glycan	Saccharide	28%
Region 10	ranthipeptide	3,395,253	3,416,656	freyrasin	RiPP	100%
Region 11	NRPS	3,699,234	3,762,117	fusaricidin B	Polyketide+NRP:Lipopeptide	100%
Region 12	RRE-containing	3,982,629	4,004,083			
Region 13	lanthipeptide-class-i , cyclic-lactone-autoinducer	4,630,590	4,657,942	paenibacillin	RiPP:Lanthipeptide	90%
Region 14	transAT-PKS , NRPS	4,673,693	4,751,074			
Region 15	proteusin	4,837,844	4,858,080			
Region 16	NRPS , transAT-PKS	4,890,525	4,990,509			
Region 17	lassopeptide	5,025,669	5,049,736	iturin	NRP+Polyketide	22%
Region 18	cyclic-lactone-autoinducer	5,099,878	5,120,408			
Region 19	lanthipeptide-class-i	5,463,080	5,490,089	paenilan	RiPP	100%
Region 20	phosphonate	5,614,046	5,629,294			
Region 21	NRPS-like , cyclic-lactone-autoinducer	5,775,107	5,837,237			

C. *Pseudomonas protegens* PS1 (NZ_CP081490.1) 17 regions



Region	Type	From	To	Most similar known cluster		Similarity
Region 1	RiPP-like	36,120	46,965			
Region 2	T3PKS	300,551	341,600	2,4-diacetylphloroglucinol	Polyketide	100%
Region 3	redox-cofactor	609,759	631,924	lankacidin C	NRP+Polyketide	13%
Region 4	NAGGN	1,865,194	1,880,026			
Region 5	NRPS	2,002,788	2,055,804	Pf-5 pyoverdine	NRP	21%
Region 6	ranthipeptide , NRPS , NRP-metallophore	2,087,507	2,192,118	Pf-5 pyoverdine	NRP	39%
Region 7	betalactone	2,306,133	2,329,357	fengycin	NRP	13%
Region 8	NRP-metallophore , NRPS	2,825,954	2,877,088	enantio-pyochelin	NRP	100%
Region 9	thiopeptide	3,044,628	3,080,483	3-thiaglutamate	RiPP	80%
Region 10	transAT-PKS , NRPS	3,164,116	3,245,753	pyoverdine DC3000	NRP	3%
Region 11	methanobactin	3,411,233	3,432,620	methanobactin	RiPP	50%
Region 12	hydrogen-cyanide	3,859,615	3,872,590	hydrogen cyanide	Other	100%
Region 13	NRPS , phosphonate	4,315,825	4,390,345	orfamide A/orfamide C	NRP:Cyclic depsipeptide	88%
Region 14	RiPP-like	5,328,510	5,340,450			
Region 15	RiPP-like	5,374,165	5,385,055			
Region 16	arylpolyene	6,335,613	6,379,230	APE Vf	Other	40%
Region 17	aminopolycarboxylic-acid	6,642,377	6,658,422	EDHA	Other	44%

(caption on next page)

Fig. 2. Biosynthetic gene clusters (BGCs) were identified by antiSMASH version 7.1.0 from whole genome sequences. **(A)** *B. subtilis* NCIB 3610 (NZ_CP094361.1). Fourteen BGCs were found, including surfactin, fengycin, bacilysin, bacillibactin, and T3PKS. *B. subtilis* NCIB 3610 is a representative strain in subtilis clade. (B) *P. polymyxa* ATCC 842 (NZ_CP024795.1). Twenty-one BGCs, including fusaricidin and polymyxin, were found. *Paenibacillus polymyxa* ATCC 842 is a representative strain in *P. polymyxa* complex. (C) *P. protegens* PS1 (NZ_CP081490.1). Seventeen BGCs were found, including 2,4-diacetylphloroglucinol (DAPG) and orfamide. *Pseudomonas protegens* PS1 is a representative strain of the *P. corrugata* subgroup under the *P. fluorescens* complex. Accession numbers were obtained from NCBI and submitted to antiSMASH on November 26, 2023 (https://antismash.secondarymetabolites) to search the biosynthetic gene clusters [90].

mycelial growth [56].

2.1.3. Volatile compounds

Endophytic bacteria also release volatile organic compounds (VOCs), which are reported to be able to inhibit phytopathogenic fungi, bacteria, and nematodes [57]. *Pseudomonas putida*, isolated from black pepper root, inhibited *Phytopthora capsici*, *Athelia rolfsii, Giberella moniliformis*, *R. solani*, *Pythium myriotylum*, and *Colletotrichum gloeosporioides* by its VOCs [58]. *The B. subtilis strain DZSY21, isolated from Eucommia ulmoides leaves,* inhibited *Curvularia lunata* by producing VOCs, isopentyl acetate, and 2- heptanone [59]. VOCs of *B. velezensis* ZSY-1 strongly suppressed *F. oxysporum, Alternaria solani*, *B. cinerea*, *Colletotrichum lindemuthianum* [60].

2.1.4. Siderophores

Some endophytes, including *Bacillus*, *Paenibacillus,* and *Pseudomonas*, can produce active low molecular weight compounds that can chelate iron (Fe), supply it in plant-available form, and deprive pathogens of iron [47]. Siderophores produced by endophytes such as hydroxymate, phenolate, catecholate, and pyoverdine have exhibited biocontrol activity [61–63]. For example, Yu et al. [64] reported that *B. subtilis* strain CAS15 inhibited fungal isolates of *Colletotrichum*, *Fusarium*, *Magnaporthe*, *Pythium,* and *Phytopthora* through bacillibactin (catecholate type siderophores) production.

2.1.5. Interruption of quorum sensing

Quorum sensing is a process that regulates activities like crosstalk among the cells, biofilm formation, reproduction, mutualism, adaption, and pathogenesis [65]. Some endophytes have been identified as having interrupted phytopathogenic signaling pathways by quenching quorum sensing [66]. *Rhodococcus corynebacterioides, Pseudomonas aeruginosa*, and *Stenotrophomonas maltophilia*, which were isolated from various plants, destroyed quorum-sensing compounds, namely 3-hydroxy palmitic acid methyl ester of *R. solanacearum*, and thus suppress eggplant wilt [67].

2.1.6. Competition for nutrients and space

Endophytic bacteria may also inhibit pathogens by competition for nutrients and space. Lastochkina et al. [68] reported that *B. subtilis* suppressed *Phytopthora infestans* and *F. oxysporum* by competing effectively for nutrients and space inside the potato tubers.

2.2. Indirect biocontrol mechanisms of endophytic bacteria

The indirect biocontrol mechanism involves the induction of plant defenses associated with microbes. Two kinds of induced defenses have been proposed, namely induced systemic resistance (ISR) and systemic acquired resistance (SAR), based on the hormonal implications and the elicitor type [69]. ISR is triggered by rhizobacteria or other non-pathogenic microbes, while pathogenic microbes or chemical compounds trigger SAR [70]. ISR is operated by the jasmonic acid (JA) or ethylene (ET) pathways, and SAR is regulated by the salicylic acid (SA)-dependent signaling pathways following pathogenesis-related (PRs) proteins gene expression [71–73]. However, ISR may also depend on both SA and JA/ET signaling processes. The ISR driven by *B. cereus* strain AR156 depended on SA and JA/ET signaling process and NPR1 [74]. Another study showed that endophytic *B. subtilis*, producing antifungal lipopeptides (fengycin and iturin), protected maize from *F. moniliforme* and induced PR genes (PR-1 and PR-4) in maize [34].

Endophytic bacteria-mediated ISR can protect plants from phytopathogens [19,75]. For example, ISR was developed in saffron against *F. oxysporum* by *Burkholderia gladioli* [25], in grapevine and tomato against *B. cinerea* [76], and *Verticillium dahliae* [77] by *Pseudomonas* sp., in oak against *Ceratocystis fagacearum* by *P. putida and P. denitrificans* [78], in tomato against *F. oxysporum* f. sp. *radicis-lycopersici* by *P. fluorescens* [79], and pea against *F. oxysporum* f. sp. *pisi* by *B. pumilus* [80].

3. Biocontrol mechanisms of *Bacillus*

The *Bacillus* genus is ubiquitous and can live in soil, water, and air, on the surface, inside plant and rhizosphere, gastrointestinal tracts, and other extreme environments [21,81]. Some *Bacillus* are used in agriculture for easy industrial production, satisfactory biocontrol efficacy, and environmental safety [82–84]. The species of *Bacillus* species have divergent secondary metabolisms and various antagonistic compounds. *B. subtilis* strains may contain up to 5 % of their whole genome for secondary metabolite synthesis [85]. *B. amyloliquefaciens* FZB42 comprises 8 % of the genome for secondary metabolites synthesis such as polyketides, lipopeptides, antimicrobial peptides antimicrobial peptides, siderophores, and bacteriocins [86,87].

Previous studies revealed that biosynthetic gene clusters (BGCs) are phylogenetically conserved in the *Bacillus* genus, and multiple species or clade-specific molecules have been discovered [88]. Xia et al. [89] reported that BGCs distribution is related to their phylogenetic position based on large-scale *Bacillus* genome analysis. The BGCs in the cereus clade include non-ribosomally synthesized

peptides (NRPS), fengycin, bacteriocin, bacillibactin, and petrobactin; thurincin, polyoxypeptin, and zwittermicin were found in some genomes of *B. thuringiensis* and *B. cereus* [89]. In the subtilis clade, fengycin, surfactin, bacillibactin, bacilysin, and T3PKS are primarily present (Fig. 2. A). Each group have specific BGCs like betalactone for *B. pumilus*, subtilosin and subtilin for *B. subtilis*, macrolactin and difficidin for *B. velezensis* and *B. amyloliquefaciens* too. Some genomes of *B. velezensis* and *B. amyloliquefaciens* contain plipastatin, mersacidin, and plantazolicin, and lichenysin may be produced by *B. licheniformis* [89]. In the megaterium clade, siderophore, surfactin, and T3PKS were found, and some can produce lanthipeptide, paeninodin, or bacteriocins. The major BGCs in the circulans clade were identified as T3PKS, and some produce siderophore, lanthipeptide, and bacteriocin [89]. The secondary metabolites of the *Bacillus* genus include NRPS, polyketide and lipopeptides, bacteriocins, and siderophores. NRPS and lipopeptides are a highly heterogeneous group consisting of amino acids, amino- or hydroxyl- fatty acids with various hydrocarbon chains, and sometimes these go under acylation, glycosylation, and methylation [81].

B. subtilis combines many useful features like plant colonization competence, growth-promoting activities, suppression of pathogens, and ISR activation [83,91]. The motile nature and biofilm formation are very important for *B. subtilis* to colonize roots and for biocontrol of phytopathogens [92]. Furthermore, phytohormones, lipopeptides, siderophores, and volatile compounds enable *B. subtilis* to promote plant growth and induce the immune system of plants [93]. According to Cawoy et al. [94], some *B. subtilis/B. amyloliquefaciens* strains can inhibit fungal pathogens. Iturins and fengycins are key factors for fungal inhibition [95,96]. The fengycin (*fen*) gene cluster constitutes *fenA*, *fenB*, *fenC*, *fenD*, and *fenE*. All five genes are conserved in *B. siamensis* and *B. velezensis*, while *B. amyloliquefaciens* has *fenA* and *fenE* [97].

Fengycin mechanisms involving cell death of the pathogens may be related to interactions with the cell membrane and cell permeability modification [98]. Scanning electron microscopy (SEM) and transmission electron microscopy (TEM) revealed that the application of *B. subtilis* BS155 synthesized fengycin caused damage to *M. oryzae* hyphae, cytoplasm, plasma membrane, and loss of cell membrane integrity, resulting in cell death [98]. Fengycin can be applied to manage rice blast caused by *M. grisea* [98], barley head blight caused by *F. graminearum* [99], cucurbit powdery mildew caused by *Podosphaera fusca* [100], grey mold caused by *B. cinerea* [101] and maize disease caused by *Rhizomucor variabilis* [102], etc. Iturin LPs family includes iturin A, C, D, and E, bacillomycin D and F, bacillopeptin, and mycosubtilin [103]. Bacillomycin-D produced by *B. velezensis* showed antagonism against various pathogens, such as *Xanthomonas campestris* pv. *cucurbitae* [104], *F. graminearum* [105], *Aspergillus flavus* [106], and *F. oxysporum* f. sp. *cucumerinum* [107]. SEM and TEM examination determined that bacillomycin-D altered the morphology of the cytoplasmic membrane, cell wall, conidia, and hyphae of *F. graminearum*. Bacillomycin-D of *B. velezensis* induced the expression of thioredoxin and glutathione reductase genes of *F. graminearum,* which are involved in reactive oxygen species (ROS) synthesis. The genes encoding catalase and peroxidase enzymes were downregulated when *F.* graminearum was treated with bacillomycin-D. The bacillomycin-D-induced ROS was associated with *F. graminearum* cell death [105]. *Bacillus* strains may produce huge amounts of surfactins but have less fungal inhibitory action. It has antibiotic actions [107,108], with rare antifungal activity [94]. Gu et al. [92] reported that *B. subtilis* produced subtilosin A and bacilysin and controlled *Acidovorax citrulli,* causing fruit blotch. Agarwal et al. [109] found that *B. pumilus* can inhibit *R. solani* and *F. oxysporum* by chitinase and surfactin production. An illustration of *Bacillus* lipopeptides like fengycin and iturin-driven antifungal mechanisms of *Bacillus* is shown in Fig. 3.

4. Biocontrol mechanisms of *Paenibacillus*

Paenibacillus is well recognized for its secondary metabolites, including nonribosomal lipopeptides, polyketides, lassopeptides,

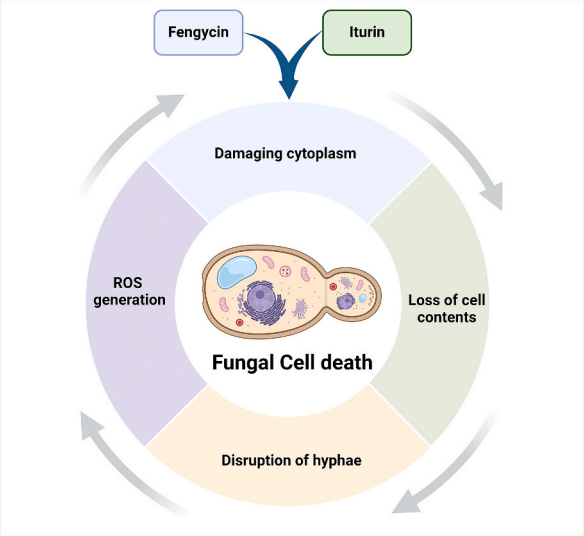


Fig. 3. A generalized schematic representation of antifungal mechanisms of lipopeptides synthesized by *Bacillus*.

bacteriocins, and lantibiotics, which are valuable in medicine and agrobiotechnology [52,110]. The most found bioactive compounds in *Paenibacillus* are lipopeptides with diverse linear and cyclic structures with peptide chains containing 6 to 13 amino acids and variable fatty acid chains [52]. These lipopeptides include fusaricidins and LiF-antibiotics [111,112], paenilipoheptins [113], octapeptins [114,115], polypeptins [114], pelgipeptins (cyclic liponanopeptides, β-hydroxy fatty acid) [116], polymyxins, tridecapeptins [114] and paenibacterins [117]. *P. polymyxa* bacteria are potent plant growth-promoter colonizing rhizoplane [118] and can also live as endophytes inside the plant [20]. These strains can synthesize four lipopeptides: polymyxins, fusaricidins, paenilipoheptins, and tridecaptins. All of these are comprised of various structural homologs. In specifics, fusaricidins are an uncommon complexity of isoforms, resulting in a broad range of parallel substances with strong antifungal activities. Fusaricidins and polymyxins biosynthesis is accomplished non-ribosomally at multifunctional protein templates [52,119]. Most *P. polymyxa* complex members possess the biosynthetic gene clusters of fusaricidins and polymyxin (Fig. 2. B).

Fusaricidin synthesis is controlled by the fusaricidin biosynthetic (*fus*) gene cluster. The cluster contains eight genes in the order of *fusG*, *fusF*, *fusE*, *fusD*, *fusC*, *fusB*, *fusA*, and *fusTE*; mutation analysis revealed that genes *fusG*, *fusF*, *fusE*, *fusD*, *fusC*, *fusB,* and *fusA* except *fusTE* were all responsible for the antifungal actions [42]. Among the eight genes, *fusA* is needed for the synthesis of cyclic polypeptide moiety, and the *fusG*, *fusF*, *fusE*, *fusD*, *fusC,* and *fusB* are essential for the synthesis of lipid moiety of fusaricidins. *fusG*, *fusF*, *fusE*, *fusD*, *fusC*, *fusB,* and *fusA* are arranged independently in a single operon, and its promoter transcribed fusTE [42]. The *fusA* gene contains modules of six amino acids activation and condensation to form a complete fusaricidin peptide chain [120].

After discovering fusaricidins [121], other researchers conducted further detailed studies [122,123]. Fusaricidins are great broad-spectrum antifungal compounds against a range of phytopathogenic fungi. For example, Li and Chen [42] reported that fusaricidin produced by *P. polymyxa* WLY78 inhibited the fungal development of *F. oxysporum* f. sp. *cucumerinum* causal agent of cucumber wilt. Its fusaricidin inhibited spore development and damaged *F. oxysporum* f. sp. *cucumerinum* hyphae. It also elicited the plant's systemic resistance against fungal pathogens. Beatty and Jensen [124] observed that *P. polymyxa* PKB1 produced fusaricidin, which inhibited the *Leptosphaeria maculans*, a fungus of canola that causes blackleg disease. Mousa et al. [125] showed that fusaricidin produced by endophytic *Paenibacillus* inhibited *F. graminearum*, a causal agent of gibberella ear rot in maize. In a recent study, RNA-seq results revealed that fusaricidins producing *P. polymyxa* AF01 arrested some of the transcription as well as translation, hampered the structural dynamics of RNA and DNA, interrupted energy production and or conversion and transduction of signals, caused ROS accumulation, ultimately inhibited the biosynthesis of cell wall, altered membrane permeability and restricted protein biosynthesis [126]. A proposed mode of actions of fusaricidins has been illustrated based upon previous studies (Fig. 4).

5. Biocontrol mechanisms of *Pseudomonas*

The *Pseudomonas* genus consists of about 428 species (https://www.ncbi.nlm.nih.gov/genome/?term=pseudomonas, accessed on March 23, 2024) occurring in diverse habitat or niches including soils, water, animal guts, and plant tissues [127]. Many *Pseudomonas*

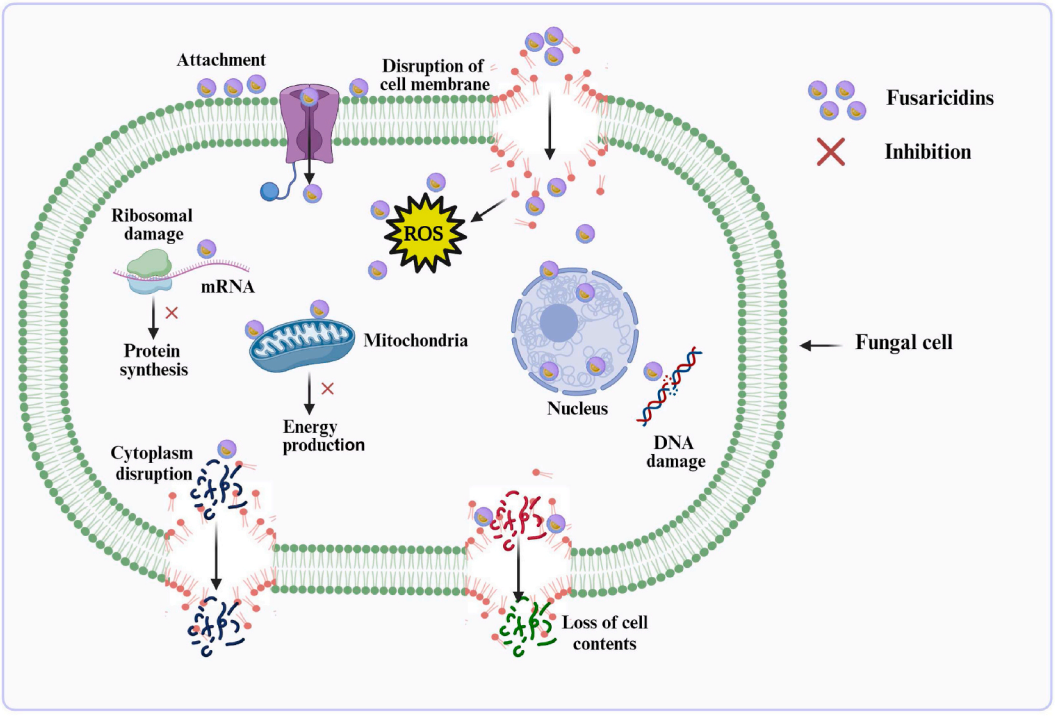


Fig. 4. Schematic representation of possible mechanisms of fusaricidins, most commonly produced by the members of the *P. polymyxa* complex.

species were isolated and characterized as PGPB for their useful functions to plants [128]. Many *Pseudomonas* species are associated with plants belonging to the *P. fluorescens* lineage, and they phylogenetically fall into five groups such as *P. fluorescens*, *P. putida*, *P. syringae*, *P. lutea,* and *P. asplenii* [129]. Among these, some are useful for biocontrol or growth promotion, especially the species under the *P. fluorescens* group, and some others show plant pathogenicity, mostly under the *P. syringae* or *P. asplenii* groups [130]. The plant-beneficial *Pseudomonas* exhibits plant benefits in various ways: direct pathogens inhibition, plant resistance development, effects on plant growth, utilization of minerals, and environmental stress tolerance [131].

Non-ribosomally synthesized polyketides and cyclic lipopeptides are major secondary metabolites with antimicrobial activity synthesized by PGPB *Pseudomonas* [132,133]. *P. protegens* strain Pf-5, *P. kilonensis* strain F113, and *P. fluorescens* strains SBW25 and 2P24 produced 2,4-diacetylphloroglucinol (DAPG), Orfamide, viscosin, phenazines, pyrrolnitrin, pyoluteorin, and amphisin showing direct phytopathogenic inhibition [134,135]. The cyclic lipopeptides may contribute to biofilm formation, swarming motility, pathogen virulence, and antifungal, antibacterial, anti-oomycete, antiviral, insecticidal, and anti-carcinogenic attributes [132,136]. The DAPG is a widely studied secondary metabolite with antibacterial, antifungal, antiviral, and antihelminthic properties [137]. Some strains of *P. protegens* and *P. corrugata* subgroups under the *P. fluorescens* complex comprise the DAPG biosynthetic gene cluster [135]. The biosynthetic gene clusters of a *P. protegens* strain are given here (Fig. 2. C). The phl gene cluster controls the DAPG production and consists of *phlACBDE* operon associated with *phlF*, *phlG*, *phlH*, and *phlI* genes [138,139]. The *phlD* is essential for monoacetylphloroglucinol (MAPG) synthesis, whereas *phlA*, *phlB,* and *phlC* are associated with transforming MAPG to DAPG [138].

Kwak et al. [140] discovered the action mechanisms of DAPG by using a mutant library of *Saccharomyces cerevisiae,* and they identified 231 mutants that were DAPG sensitive. The selected mutants were subjected to chemical, biochemical, and genetic analyses, and they reported three prime physiological activities relevant to DAPG sensitivity: membrane permeability, ROS regulation, and homeostasis of cells. According to Stepanov et al. [141], the antifungal actions of DAPG include damaging cellular permeability, malfunctioning of H + ATPase, and disturbance of mitochondrial respiration. The primary adverse effects of DAPG are respiration intervention and ATP synthesis, leading to growth inhibition [142]. Ali et al. [45] observed a DAPG-producing strain, *P. bijieensis* XL17, belongs to the *P. corrugata* subgroup, has damaged cell membrane and cytoplasm, causing cell wall leakage, and tends to lose cell organelles. An illustration of the probable fungal inhibition mechanism of DAPG is given below (Fig. 5).

In addition to secondary metabolite-driven antagonism against pathogens, biocontrol control of *Pseudomonas* is also connected to ISR and siderophore-mediated iron competition [143]. *P. simiae* strain WCS417, including other strains, showed colonization competence in plant roots and triggered ISR, resulting in higher protection against plant pathogens [143]. The Type VI secretion system (T6SS) in *Pseudomonas* spp. is important for its biocontrol activity. The T6SS is a syringe-like structure resembling a phage tail capable of secreting effector proteins into targeted prokaryotic and eukaryotic cells [144,145]. This system has been recognized as a powerful antifungal weapon, and fungal-specific effector proteins, Tfe1 and Tfe2, have been identified. These effector proteins act through specific mechanisms in various fungal species by causing cell death. Tef1 causes the depolarization of the plasma membrane, and Tef2 interrupts nutrient uptake and induces autophagy [146,147].

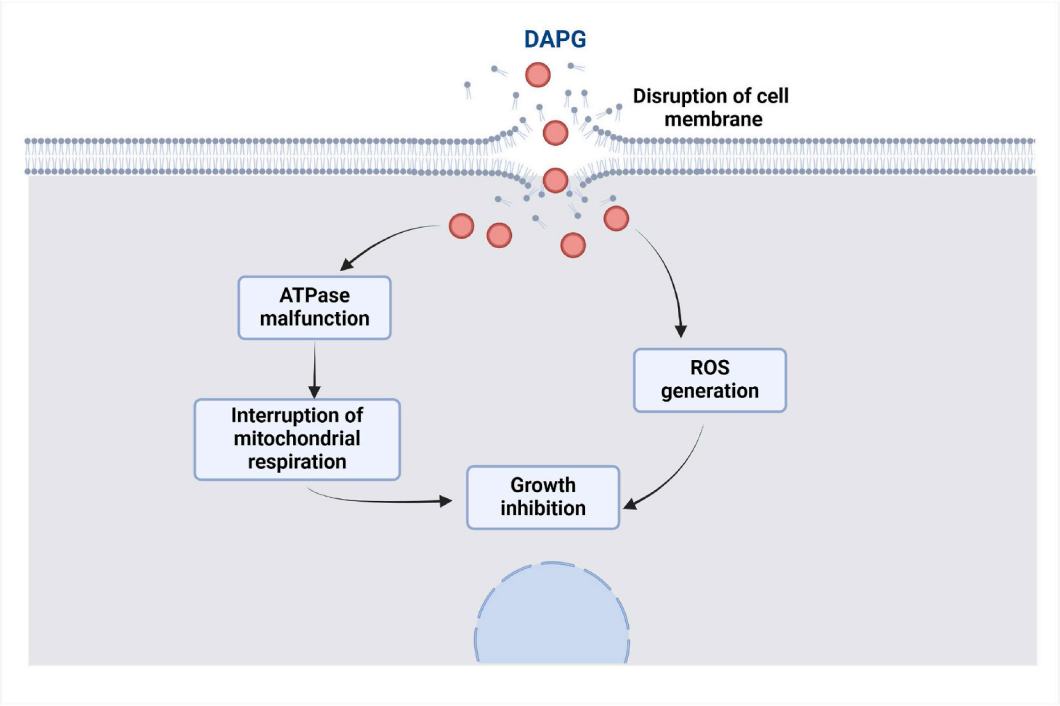


Fig. 5. An illustration of possible antifungal mechanisms of DAPG.

6. Endophytic bacteria in plant growth promotion

The PGPB includes free-living bacteria that may establish symbiosis with plants (e.g., *Rhizobia* spp.), endophytic bacteria in plant tissues, and cyanobacteria [17,31,148]. Despite the differences within different groups, all these bacteria utilize similar mechanisms. These bacteria contain some plant-growth promoting (PGP) traits. PGPB enhances plant growth by acquiring nutrients or phytohormone modulation or inhibiting various plant pathogens [83,149] (Fig. 1). Some endophytic bacteria bearing plant growth-promoting attributes are listed in Table 2.

6.1. Nutrient acquisition

Nutrient or resource acquisition is the best-studied phenomenon of PGPB by which bacteria can provide nutrient resources (nitrogen, iron, phosphorus, etc.) in available form to plants [32,161,162]. Some endophytic bacteria can biologically fixed atmospheric nitrogen to the available state for utilization by plants using nitrogenase [163]. Nitrogen-fixing bacteria, such as *Azospirillum brasilense* and *Azoarcus* sp. BH72, *Burkholderia* spp., *Herbaspirillum seropedicae,* and *Gluconacetobacter diazotrophicus* increased plant growth by N_2 fixing in controlled environments [164].

Endophytic bacteria may solubilize fixed phosphates and become available to plants [161,162,165]. These endophytic bacteria

Table 2
List of plant growth-promoting endophytic bacteria.

Strain	Origin	Test plants	PGP traits	References
Bacillus				
B. subtilis 2S	Maize stem	Maize	IAA Siderophore	[21]
B. subtilis 135	Honeysuckle root	Wheat	IAA Siderophore	[150]
B. cereus EPP5	Pearl millet stem	Pearl millet	IAA Siderophore Phosphate solubilization Potassium solubilization	[151]
B. amyloliquefaciens EPP62	Pearl millet root	Pearl millet	IAA Siderophore Phosphate solubilization Potassium solubilization	[151]
B. thuringiensis CR71	Tomatillo root	Cucumber	IAA Siderophore	[152]
B. altitudinis SB001	Sweet-grass root	Tobacco Maize Soybean	IAA	[153]
Paenibacillus				
P. polymyxa SK1	Tiger lily bulb	Tiger lily	IAA Siderophore Nitrogen fixation Phosphate solubilization	[154]
P. polymyxa 122	Honeysuckle root	Wheat	IAA Siderophore Phosphate solubilization	[155]
P. peoriae RP51	Black locust nodule	Wheat	IAA Siderophore Nitrogen fixation Phosphate solubilization	[156]
Pseudomonas				
P. bijieensis XL17	Rape crown gall	Rice	IAA Phosphate solubilization	[45]
Pseudomonas sp. CI-3	Chickpea root	Chickpea	IAA Siderophore Phosphate solubilization	[155]
Pseudomonas sp. n00132	Rice leaf	Rice	IAA Siderophore Phosphate solubilization	[156]
P. aeruginosa KAS6	Pearl millet seed	Pearl millet	IAA Phosphate solubilization	[157]
P. flourescens L228	Elephant grass leaf	Pea	Phosphate solubilization	[158]
P. flourescens L321	Elephant grass leaf	Rapeseed	IAA Siderophore Phosphate solubilization	[159]
P. aeruginosa Ld-08	Lily bulb	Lily	IAA Siderophore Phosphate solubilization	[160]

may also assimilate soluble phosphorus by preventing phosphate fixation and its adsorption in phosphate-limiting conditions [166]. In this way, they can serve as reservoirs of phosphorus for plants.

Endophytic bacteria produce siderophores, chelate insoluble ferric ions, and supply iron to plants [167]. *Pseudomonas* strain GRP3, a siderophore-producing bacterium, was inoculated in mung beans under iron deficit conditions, which increased chlorophyll levels compared to untreated plants [168]. *P. flourescens* synthesized Fe-pyoverdine complex was uptaken by *Arabidopsis thaliana,* increasing iron levels in plants with increasing plant growth [169].

6.2. Modulating phytohormones

Endophytes produce phytohormones that regulate plant physiology, growth and development [31,170,171]. Indole-3-acetic acid (IAA), cytokinins, gibberellins and ethylene are important hormones in the interactions between plants and bacteria [84,161,167, 171]. IAA of endophytic bacteria increases root volume, surface area, and lateral roots in plants [172]. For example, Tsavkelova et al. [173] observed that the IAA of orchids inhabiting endophytic bacteria had effects on increasing root length and number of roots of kidney beans used during bioassay.

Biotic and abiotic stresses can trigger ethylene synthesis in plants [31][84]. A higher level of ethylene may deter plant root development. Endophytic bacteria synthesize 1-aminocyclopropane-1- carboxylate (ACC) deaminase and can hydrolyze ACC, the prior product of plant ethylene. The ACC deaminase-producing bacteria break ACC into α-ketobutyrate and ammonia [174]. Hence, these bacteria can improve plant growth by ameliorating stress conditions [14].

Endophytic bacteria can also produce cytokinins and gibberellins [84,171,175]. Cytokinins regulate cell division, seed germination, elongation of the root, differentiation of chloroplast and xylem, axillary and flowering bud growth, fruit set, leaf senescence, and increase biotic and abiotic tolerance [176–181]. The root inoculation of *P. flourescens* strain G20–18, which can produce cytokinins, promoted tomato growth and increased drought tolerance [182]. Endophytic *P. resinovorans* strain Gp e1 and *P. polymyxa* strain Gp e2 were shown to produce cytokinin-like substances [183]. Gibberellins enhance seed germination, promote stem and leaf growth, develop flowers and fruits, and restrict plant ageing [184,185]. *B. amyloliquefaciens* RWL-1 and *P. pseudomonas* strains improved plant growth by gibberellins production [186,187].

6.3. Stress tolerance

Biotic and abiotic stresses reduce crop growth and in some scenarios, give negative effects to soil fertility and health [17,188]. Endophytic bacteria can inhibit pathogens through biocontrol potentials and improve systemic plant resistance. They can reduce abiotic stresses by osmotic adjustments, antioxidant enzyme production, phytohormone alteration, and modification of plant morphology and signal system [17,188,189]. Heat-tolerant endophytes and rhizobacteria like *B. amyloliquefaciens* and *P. putida* compensate for heat stress in rice and wheat by modulating antioxidant defense enzymes and plant hormones [190,191]. Endophytic *B. cereus* enhanced rice salinity tolerance by modulating IAA, abscisic acids, and gibberellins [20]. *P. polymyxa* CR1 primed drought stress tolerance and root growth of soybean and arabidopsis [192]. It was found that endophytes can transfer and solubilize nutrient elements like phosphorus, nitrogen, potassium, and other micronutrients and make them available to plants [193,194].

7. Future perspectives and the suggested screening approaches to identify biocontrol and plant growth-promoting agents

Endophytic bacteria are capable of living inside the plant system. Therefore, it is a great opportunity to select the most promising ones from these bacterial diversity for applications in sustainable agriculture. Research on effectiveness, perspectives, and implications for the usage of endophytic bacteria in biological control are crucial, in addition to the antifungal activity. Many endophytic bacteria have been selected for biocontrol and plant growth promotion. However, most of them were evaluated under *in vitro* conditions, and further operational evaluation should be confirmed under field conditions. When proven successful, these bacteria can be used to replace the agrochemicals in delivering natural biocontrol functionality in agriculture.

In this review, we suggested a rapid approach to screen and identify the broad-spectrum biocontrol bacteria belonging to various known groups, for example, *Bacillus subtilis* clade, *Paenibacillus polymyxa* complex, and *Pseudomonas fluorescens* complex, etc. The screening strategies may include the following steps:

First step: Confrontation cultures of bacterial isolates and pathogens screen out antimicrobial bacteria.

Second step: 16S rRNA gene sequences analysis phylogenetically to identify antimicrobial strains of known taxonomic groups, which are most probably able to produce plant growth-promoting IAA, fix N_2, and produce broad-spectrum antimicrobials.

Third step: Matrix-assisted laser desorption ionization-time of flight-mass spectrometry (MALDI-TOF-MS) analyses to identify lipopeptide producers.

Fourth step: PCR amplification and sequencing of key biosynthesis genes, such as *phlD* and *nifH*, to identify a key biocontrol or plant growth-promoting trait.

Fifth step: Gnotobiotic assay of plant seedlings, a biocontrol strain, and a target pathogen to screen biocontrol strains with plant colonizing capacity and *in planta* biocontrol ability.

Sixth step: Field trials using promising biocontrol and plant growth-promoting strains to determine practical application.

8. Conclusion

Endophytic bacteria are effective and useful alternative biological tools to agrochemicals. They can control phytopathogenic fungi and promote plant growth without negatively impacting the agroecosystem. The underlying antifungal mechanisms mostly involve lipopeptides and polyketides. Fengycin, fusaricidins, and DAPG are key metabolites for antifungal activity in the case of endophytic *Bacillus*, *Paenibacillus*, and *Pseudomonas*, exhibiting dual biocontrol and plant-growth promotion functionality. Proper screening of these endophytic bacteria is crucial. Most studies on endophytic bacteria-driven biocontrol and plant growth promotion are conducted under laboratory conditions. Moving forward, more endophytic bacteria should be screened initially in the laboratory, and tests should be extended to realistic and operational conditions (e.g. farm level) for their utilization in developing sustainable agriculture.

Data availability

No data was used for the research described in the article.

Ethics declarations

Review and approval by an ethics committee was not required for this study because it is a literature review and does not address the ethical considerations of animal, cell, and human experimentation.

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CRediT authorship contribution statement

Md Arshad Ali: Writing – original draft, Data curation, Conceptualization. **Temoor Ahmed:** Writing – review & editing, Conceptualization. **Ezzeldin Ibrahim:** Writing – original draft, Data curation. **Muhammad Rizwan:** Writing – original draft, Data curation. **Khim Phin Chong:** Writing – review & editing, Supervision, Conceptualization. **Jean Wan Hong Yong:** Writing – review & editing, Supervision.

Declaration of generative AI and AI-assisted technologies in the writing process

While preparing this work, the author(s) used Grammarly Software to improve the language. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the publication's content.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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