BIOTECHNOLOGY & BIOTECHNOLOGICAL EQUIPMENT, 2017
VOL. 31, NO. 3, 446–459
http://dx.doi.org/10.1080/13102818.2017.1286950

Taylor & Francis
Taylor & Francis Group

REVIEW; AGRICULTURE AND ENVIRONMENTAL BIOTECHNOLOGY

OPEN ACCESS

Bacillus species as versatile weapons for plant pathogens: a review

Jamil Shafi, Hui Tian and Mingshan Ji

Department of Pesticide Science, Plant Protection College, Shenyang Agricultural University, Shenyang, Liaoning, P. R. China

ABSTRACT

Plant pathogens are the main threat for profitable agricultural productivity. Currently, chemical-based pesticides are thought to be an effective and reliable agricultural management measure for controlling pests. Chemical pesticides are highly effective and convenient to use but they are a potential threat for the environment and all kinds of life on earth. Therefore, the use of biological control agents for the management of plant pathogens is considered as a safer and sustainable strategy for safe and profitable agricultural productivity. *Bacillus*-based biocontrol agents play a fundamental role in the field of biopesticides. Many *Bacillus* species have proved to be effective against a broad range of plant pathogens. They have been reported as plant growth promoter, systemic resistance inducer, and used for production of a broad range of antimicrobial compounds (lipopeptides, antibiotics and enzymes) and competitors for growth factors (space and nutrients) with other pathogenic microorganisms through colonization. The aim of this article is to present the biocontrol potential of *Bacillus* species in relation with their antagonizing attributes against plant pathogens. These attributes include production of lipopeptides, antibiotics and enzymes as well as plant growth promotion and systemic induced resistance.

ARTICLE HISTORY
Received 29 April 2016
Accepted 23 January 2017

KEYWORDS
Bacillus species; lipopeptides; antibiotics; systemic induced resistance; colonization; mode of action

Introduction

It is of essence to control plant diseases for the production of quality and abundance of food, feed and fibre for maintaining a healthy and rapidly growing world population. Different kinds of plant disease management strategies may be adopted for the management or eradication of plant diseases. Most of the agriculturists in the world often depend on chemical-based pesticides and fertilizers for bounty agricultural output. Over the past centuries, agrochemicals have played a very important role for improving crop quality and quantity. However, during recent years, there is a change in attitude of people towards chemical-based fertilizer and pesticides due to the emerging hazards of environmental pollution and pesticide residual effects on human health and also on the earth ecosystem. As a result of these problems, stringent laws and regulations have been imposed for the safe use of agrochemicals. Consequently, scientists diverted their attention towards the alternative of synthetic agrochemicals which led to the development of biopesticides [1,2].

The earlier research work has repeatedly reported that numerous plant pathogenic diseases can be controlled by natural antagonistic microorganisms [3]. The relationship between antagonistic microbes and plant pathogens may be composite. It may involve the production of antipathogenic chemicals, competition for space and other necessities or triggering the host defensive mechanism and predation [4]. However, some strains of these microbes have abilities to overcome plant pathogenic diseases under various cropping environments and some of them have abilities to control a broad range of plant pathogens. Rigorous research activities have discovered several microorganisms for the development of biopesticides at commercial level.

Among the bacterial antagonists, many belong to the genus *Bacillus* and there are some other important genera but are of lesser applied importance than *Bacillus* [5]. The use and number of antagonistically important *Bacillus* species is increasing very rapidly. *Bacillus* species have a unique ability to replicate rapidly, resistant to adverse environmental conditions as well as they have broad spectrum of biocontrol ability. Volatile compounds produced by *B. subtilis* also play an important role in plant growth promotion and activation of plant defence mechanism by triggering the induced systemic resistance (ISR) in plants [6]. According to Denner and Gillanders [7], the US Food and Drug Administration (US FDA) declared *B. subtilis* as GRAS (generally recognized as safe) organisms for its use in food processing industries. Endosporic and enzymatic products of *B. subtilis* were found highly active against many fungal pathogens.

CONTACT Mingshan Ji jimingshan@163.com; jimingshan@syau.edu.cn

© 2017 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group
This is an Open Access article distributed under the terms of the Creative Commons Attribution License (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Several microorganisms have been described as possible biocontrol agents such as *Hypericum gramineum*, *Pseudomonas flurescens* and some species of *Streptomyces* [8]. In addition, *Ulocladium atrum* and *Trichoderma* have the ability to control various bacterial and fungal diseases. They generally show control effectiveness ranging from 30% to 50%. *Bacillus* species have become attractive biological control agents due to their ability to produce hard, resistant endospores and antibiotics which control a broad range of plant pathogens [9]. This article seeks to show the biocontrol aptitudes of *Bacillus*, their antimicrobial compounds, mode of action and spectrum of these compounds and also indicate the missing aspects that should be considered for future research.

Lipopeptides- and antibiotics-based weapons

Bacillus species synthesize various types of lipopeptides based on secondary metabolites with specific activities against plant pathogens which give them a unique importance in agriculture, biotechnology and pharmaceutical industries. About 2428 antimicrobial peptides have been identified from various organisms such as bacteria (237), archaea (2), protists (7), fungi (12), plants (310), and animals (1819). Among them, 756 of such peptides have various degrees of antifungal properties [10]. The mechanisms by which microorganisms lead fungi to death include blockage, distraction and holes formation in the cell wall and cell membranes of the fungi. Also, some peptides are involved in the disintegration of fungal intracellular organs such as nucleic acid and mitochondria [11]. In addition to the production of different surfactant materials, *Bacillus* species synthesize many potent amphiphilic and surfactant lipopeptides comprising bacillomycins, iturins and mycosubtilin; with the modification of culturing conditions, these bacteria also produce fengycins or plipastatin [12]. Characterization based on the existence of L- and D-amino acids and adjustable hydrophobic studies revealed that all these fall into two categories: cyclic peptides (iturinics) and macrolactones (plipastatins, fengycins and surfactins). The iturinics cause cell leakage by inserting their hydrophobic tails in to cytoplasmic membrane and through autoaggregation to create pores in cellular membrane [13].

B. subtilis and *B. cereus* produce plipastatins to prevent phospholipase A_2 which plays an important role in different cytological process (inflammation and acute hypersensitivity) [14,15]. *B. subtilis* synthesize some other lipopeptides such as plipastatins indicated as isoformic mixture of lipopeptides that vary according to the composition of amino acids and hydrophobic tails [16]. The *Bacillus*-based lipopeptides and antibiotics are summarized in Table 1.

Haemolytic surfactant synthesized by *B. subtilis* was found to be very active against mosquitoes. Gong and his coworkers [22] studied the structure and composition of metabolites for the determination of inhibitory substances against *Aspergillus flavus* synthesized by *Bacillus subtilis* fmbJ. Four substances were found to be effective against target fungus after separation and purification of metabolic liquid produced by the bacteria. Bacillomycin D caused severe injury to both cell wall and cell membrane of fungal spores and hypha. Scanning and transmission electron microscopy showed the formation of holes by exudation of cytoplasm and cellular organelles. The purified bacillomycin significantly inhibited the spore germination (96.63%) and sporulation (98.10%) [22]. Morphological and ultrastructure studies of lipopeptides produced by *B. subtilis* strains on *Podosphaera fusca* revealed the reduction in germination of powdery mildew conidia by arresting the lipopeptides of *P. fusca* and various cellular changes [53].

Plant growth promotion as an indirect weapon

Quite apart from the antagonistic mechanism of *Bacillus* species, these microbes also have an important role in plant growth promotion by enhancing the biosynthesis of plant hormones (gibberellic acid (GA3) and indole-3-acetic acid (IAA)) that have a close relation with plant nutrient availability [54,55]. *Bacillus* species play an important role in plant growth promotion. When spore or cell suspensions *of B. subtilis* OTPB1 were applied to tomato seeds on a plastic pot, it considerably enhanced the shoot and root growth, seedling vigour and leaf area of the tomato plant. Higher level of plant growth-promoting hormones (GA3 and IAA) and defence-related enzymes (peroxidase (PO), polyphenol oxidase (PPO) and superoxide dismutase) were detected in treated plants compared with non-treated plants [56].

Many scientists have discussed that *B. subtilis* had the ability of promoting plant growth and yield by enhancing nutrient uptake by increasing the production of plant harmones and decreasing ethylene production which facilitate the bacteria in root colonization [54,55,57–60]. IAA has an important role in origination and emergence of adventitious roots. It also enhances shoot development by influencing cell expression, division and differentiation [61]. The GA3 plays it role in combination with auxin for elongation of plant and leaf bud formation [62]. These plant growth-promoting hormones enhance the nutrients uptake ability of plants and help the plant to defend against various biotic and abiotic stresses [63,64]. It was demonstrated that diluted cultural filtrate

Table 1. Summary of *Bacillus*-produced lipopeptides and antibiotics, their mode of action and target pathogens.

Bacteria	Strain	Mode of action	Active compound (s)	Target pathogen (s)	References
B. subtilis	NCIB 8872	Inhibit phospholipase A2	Antibiotics plipastatins A and B	*Fusarium oxysporium*, *Aspergillus flavus*	[17]
B. subtilis	SSE4, RB14	Disruption and solubilization of the lipid bilayer	Subtulene A, iturin A	*C. gloeosporioides and S. rolfsii*	[18,19]
B. subtilis	B47	Interrupt activity of fungal lipopeptide	Iturin A_2	Southern corn leaf blight	[20]
B. subtilis	NT-6	Blocking and destroying the cell wall and forming holes in cellular membranes	Antibacterial peptide AMPNT-6	*Vibrio parahaemolyticus*	[21]
B. subtilis	fmbJ	Cause severe injury to both cell wall and cell membrane of fungal spores and hypha	Bacillomycin D	*Aspergillus flavus*	[22]
B. amyloliquefaciens	AS 43.3	Pores formation in cell wall and cell membrane by disrupting the lipid bilayer	Surfactin, iturin, fengycin, a bacillibactin, bacilysin, bacillaene, difficidin, and macrolactin	*Fusarium* head blight in wheat	[23]
B. vallismortis	BS07	Plant growth promotion and cell wall disintegration	Surfactic and fengycin	*Pectobacterium carotovorum* SCC1, *Phytophthora capsici*, and *Colletotrichum acutatum*	[24]
B. amyloliquefaciens	WH1	Case reduction in callose production by inhibition of glucans synthase	WH1fungin	Rhizoctonia *solani*	[25]
B. subtilis	SQR 9	Inhibit mycelial growth and conidial germination of the fungal pathogen	Fengycin and bacillomycin	*F. oxysporum* f. sp. cucumerinum	[26]
B. subtilis	EU07	Inactivation of AHL by hydrolysis of AHL_5	YrvN protein-based subunit of protease, Acyl-homoserine lactonase	*F. oxysporum* f. sp. radicis-lycopersici	[27]
B. subtilis	JA	Effective against filamentous fungal pathogens but not against yeast and bacteria	Fengycin, Mycosubtilin, Subtulene	*F. graminearum*, *R. solani*, *Pythium irregulare* and *Cladosporium fulvum*	[28]
B. subtilis	JM4	Antibiotic effective against bacterial species	Subpeptin JM4-A and subpeptin JM4-B	*Salmonella*, *B. cereus* and *Staphylococcus aureus*	[29]
B. subtilis	fmbj	Disturption of lipid bilayer	Surfactic and fengycin	*B. cereus*	[30]
B. subtilis	B-916	Mycelium inhibition, a protein with ribonuclease and haemagglutinating activities	Bacisubin	*R. solani*, *Alternaria oleracea*, *A. brassicae*, *Magnaporthe grisease*, *Sclerotinia sclerotiorum*, and *Botrytis cinerea*	[31]
B. subtilis	B29	Inhibitory activity on mycelial growth	Protein-B29	*F. oxysporum*, *R. solani*, *F. moniliforme*, and *Sclerotinia sclerotiorum*	[32]
B. subtilis	LFB112	Antibiotic effect	Bacteriocin	*Pseudomonas aeruginosa*, *Escherichia coli*, *Salmonella pullorum*, *Pasteurella multocida*, *Clostridium perfringens*, *Micrococcus luteus* and *Streptococcus bovis*	[33]
B. subtilis	CMB32	Disrupt the lipid bilayer of cell wall and cell membrane	Iturin A, Fengycin, and Surfactin A	*Colletotrichum gloeosporioides*	[34]
B. subtilis	Spizizenii DSM 15029	Antibiotic activity	S-entianin and S-subtilin	Gram-positive bacterial pathogens, such as *Staphylococcus aureus* and *Enterococcus faecalis*	[35]
B. subtilis	SCK-2	Permeabilization of cell membranes	AMP IC-1	*B. cereus*	[36]
B. subtilis	14B	Disruption of the lipid bilayer structure	Bac 14B	*Alternaria solani* and other bacterial seed-borne pathogens such as wilt diseases	[37]
B. subtilis	F-29-3	The inhibition is antagonized by sterols, phospholipids and oleic acid	Fengycin	Effective against filamentous fungi but not against yeast and bacteria	[38]
B. licheniformis	H1	Bactericidal and bacteriolytic	Bacteriocin-like substance	Gram-positive bacterial pathogens such as *Listeria monocytogenes*	[39]
B. thuringiensis	Kurstaki BUPM4	Bactericidal and bacteriolytic	Bacthuricin F4	Effective against *Bacillus* species while no effect on Gram-negative microbes	[40]
B. thuringiensis	SM1	Act on cell membrane and cellular organs and inhibited DNA synthesis	Fengycin	*Candida albicans*	[41]
B. thuringiensis	Kurstaki Bn-1	Bacteriocidal or bacteriolytic effect depending on the concentration	Thuricin Bn1	*P. savastanoi*, *P. syringae*, *P. lemoignei*, *B. cereus*, *B. weinhenstephenensis*, *L. monocytogenes*, and many other *B. thuringiensis strains*	[42]
B. amyloliquefacien	LBM 5006	Abnormal conidial germination and germ tube development	Iturins-like and fengycin-like peptides	*Aspergillus* spp., *Fusarium* spp., and *Bipolaris sorokiniana*	[43]
B. amyloliquefacien	GA1		Amylolysin	*Listeria monocytogenes*	[44]
B. amyloliquefaciens	FZB42	Suppression of bacterial and fungal plant pathogens by plant growth stimulation and biosynthesis of complex and small molecules	Plantazolicin	Bacterial and fungal plant pathogens	[45]
B. polymyxa	VLB16	Cause malformation of fungal hyphae due to severe alteration of cell morphology	Antifungal protein	*R. solani* and *Pyricularia grisea*	[46]
B. pumilus			Bacitracin	*Micrococcus luteus*	[47]
B. vallismortis	ZZ185	Affect the activity of the lipopeptides of fungal pathogens	Bacillomycin D (*n*-C14) and Bacillomycin D (iso-C15)	*F. graminearum*, *A. alternata*, *R. solani*, *C. parasitica* and *P. capsici*	[48]
B. halodurans	C-125	Pore formation in lipid bilayer and potassium efflux	Two-peptide lantibiotic and Haloduracin	Wide range of Gram-positive bacterial pathogens	[49]
B. mojavensis	A21	Antibiotic and fungicidal activities	Fengycin, surfactin and pumilacidin	Gram-positive and Gram-negative bacteria, and many fungal pathogens	[50]
B. sonorensis	MT39	Antibacterial and fungal activity	Sonorensin	*L. monocytogenes* and *S. aureus*	[51]
B. coagulans	ATCC 7050	Cause leakage of ions from the microbial cells	Lactosporin	*M. luteusand*, *L. monocytogenes*	[52]

of *B. amyloliquefaciens* significantly enhanced the growth of maize seedlings. Chemical analysis of supernatant of FZB42 showed the presence of substances capable of reacting with IAA-specific antibodies [57].

Jiang et al. [65] screen out one-hundred bacterial strains for their antagonistic and growth-promotion activities and found out that *B. amyloliquefaciens* strain 54 significantly increased plant growth by enhancing the NPK and chlorophyll contents of plants. It also enhanced the level of resistance in plants against bacterial fruit blotch of cucurbitaceae crops by eliciting the defence-related gene PR1 and H_2O_2 accumulation in plant tissues [65].

Zinc solubilization, crop growth, soil biology, and zinc mobilization aptitude of *B. subtilis* strains MDSR7, MDSR11 and MDSR14 were evaluated under lab conditions. Higher soluble zinc contents and an enhancement in total organic acids were observed where MDSR7 and MDSR14 were inoculated. MDSR7 and MDSR14 cause a significant reduction in soil pH and enhanced microbial respiration as well as β-glycosidase, dehydrogenase, auxin production and microbial biomass-C in the rhizosphere of wheat and soybean. All the strains significantly enhanced the availability of zinc which enhances the plant growth and assimilation of zinc in seeds by wheat and soybean plants [66].

The *Bacillus* strain SH1RP8 showed 8% salinity tolerance when applied to sand dune plant *Peucedanum japonicum*. It enhanced 10.9% shoot growth and 51.7% dry weight when grown in general soil [67]. Lin et al. [68] isolated 33 strains of bacteria from vinegar waste. After screening through self-developed screening method, he found out that, all the *Bacillus* strains were highly antagonistic to eight fungal pathogens and had the ability to produce IAA, while five strains exhibited plant growth-promotion abilities. Wei et al. [69] evaluated 38 *Bacillus* strains for anti *Aspergillus parasiticus* ability by tip culture method. Twleve strains were selected for their anti-fungal, growth promotion and phytohormones production ability.

Nain et al. [70] studied RM-2 strain of *Bacillus* species and found that the bacterial strain had many valuable features including acetyl-CoA carboxylase (ACC) deaminization activity, P solubilization ability, fungicidal, IAA production and ammonia production activity. The stains significantly enhanced seed germination, fresh and dry weight, leaf area, root and shoot length and also seed, pods and grain yield compared with untreated control.

Valdez et al. [71] treated sunflower seeds with *B. subtilis* for investigating its effect on plant growth, soil properties and greenhouse gases emission while using urea as positive control for comparison. The results showed that after one month, root length and root–shoot fresh and dry weight were considerably higher than urea-treated plants. No significant difference was observed for CO_2 production, while N_2O production rate was higher in bacterial-treated plants compared to urea-embedded plants.

Systemically induced disease resistance

When a pathogen attacks a plant, the non-infected plant tissues acquire an ability to resist the subsequent attack; this type of broad spectrum and long-term ability of plants is known as systemic acquired resistance (SAR) [72]. Moreover, the beneficial nonpathogenic microorganisms can also trigger resistance in plants. This resistance-triggering mechanism was observed when colonization of roots by some nonpathogenic bacteria protects the above-ground plant parts from attack of various pathogenic organisms; this type of resistance response is called ISR [73]. Like SAR, nonpathogenic microbes trigger ISR which has also been shown in various plants and is effective against a broad range of diseases [74]. Park and his coworkers [75] evaluated five strains of *Bacillus* species against *Ralstonia solanacearum*. The bacterial strain EXTN-1 was proved to be effective and they also showed that reduction of disease was not due to direct antagonism but as a result of elicitation of host plant resistance genes. The main components of systemic-induced resistance are phenolic compounds, genetic and structural modifications, plant resistance activators, and activation of enzymatic weapons.

Triggering of phenolic compounds

Many experimental results have shown that *Bacillus* strains induced a broad spectrum of resistance against various bacterial and fungal plant pathogens. Park and coworkers [76] reported that *B. vallismortis* strain EXTN-1 induced SIR that was effective against a variety of bacterial and fungal diseases. Akram and Anjum [77] investigated the resistance elicitation ability of *B. fortis* 162 and *B. subtilus* 174 against *Fusarium* wilt of tomato and showed that both strains induced systemic resistance in tomato plants. They also observed the increased level of phenyl ammonia lyase (PAL), PPO and PO in bacterial-treated tomato plants and both strains significantly reduced tomato *Fusarium* wilt. Gupta and his coworkers [78] reported that cultural filtrate of *B. subtilis* strain FZB-G has the ability to trigger phytohormones precursor which plays an important role in signal transduction and activation of defence gene that results in the production of defence-related compounds [78].

Jayara and coworkers [79] investigated *B. subtilis* strain AUBS1 for systemic resistance induction against sheath blight of rice by its foliar application under greenhouse conditions and found a significantly increased level of PO and phenylalanine ammonia lyase (PAL). *B. subtilis*-treated leaves were found to have accumulation of PR proteins. They also found that the increased levels of thaumatin and β-1-3-glucanases with 17 and 30 kDa mass, respectively, play an important role for induction of resistance in rice plant.

Kloepper et al. [60] investigated the elicitation abilities of *B. subtilis*, *B. cereus*, *B. amyloliquefaciens*, *B. pasteurii*, *B. sphaericus*, *B. pumilus* and *B. mycoides* for induced resistance in tomato, muskmelon, bell pepper, sugar beet, watermelon, tobacco, *Arabidopsis* sp., loblolly pine, cucumber, and two tropical crops (green kuang futsoi and long cayenne pepper) against various pathogenic diseases under green house and field conditions. Significant reduction was observed in bacterial and spotting fungal pathogens, systemic viruses, crown-rotting, root-knot nematodes, and a stem-blight as well as blue mold, late bight and damping-off. Wang et al. [80] concluded that treatment with *B. cereus* AR156 enhances the defence related activities such as PAL, chitinase, β-1,3-glucanase, PO and PPO, and stimulated amassing of H_2O_2.

Structural and genetic activation of host plants

Triggering of systemic resistance mechanism of plants by bacterial microbes is the main cause of disease suppression by crop plants [81]. Many studies suggested that the biochemical and structural modifications in plants are key sources of disease reduction by defending pathogen attack. Structural biochemical variation can reduce the spread of pathogens in the host plant [82]. Cytological studies showed that, root colonization of pea by *B. pumilus* strain SE34 restricted *Fusarium oxysporum* f. sp. *pisi* to the epidermis and outer cortex by strengthening the cell wall and epidermal cells. In addition, the newly formed barriers contained callose and phenolic compounds which were beyond the site of infection during electron microscopy [83]. In another study, it was observed that, treatment by strain SE34 reduced fungal colonization by changing the host physiology elicited by enhancing the host cell wall density, polymorphic deposition on potential susceptible sites, obstruction of intercellular gaps and epidermal cells with amorphous and osmophilic compounds [84].

Lee and coworkers [85] screened out 78 *Bacilli* for the stimulation of ISR and found that *B. amyloliquefaciens* strain HK34 showed disease reduction up to 99.1% against Phytophthora *cactorum* when applied to root, and similar results were perceived on leaf application under field evaluation. An enhancement in expression of genes PgPR10, PgPR5, and PgCAT in plant leaves was also observed after treatment with HK34. These outcomes showed the ISR-eliciting potential of strain HK34. A mixture of PGPR strains belonging to *Bacillus* spp. were tested for elicitation of resistance against *Lycopersicon esculentum*, *Sclerotium rolfsii*, *Capsicum annuum* var. *acuminatum*, *Colletotrichum gloeosporioides* and *Cucumis sativus*. Results showed that the mixture of PGPR significantly enhanced the resistance in plant for all of the above-listed plant pathogens [86].

Activation of plant-resistance activators

Van and coworkers [87] determined that the phenotypic response of resistance induced by rhizobacteria is similar to that of pathogenically induced systemic resistance. Rhizobacterial-elicited resistance was verified against bacteria, fungi and viruses under conditions in which the rhizobacteria and pathogen were kept separately. The level of induced resistance was different for different strains of bacteria and also for different plant species. The determinants of rhizobacterial-elicited systemic-induced resistance were siderophores, lipopolysaccharides, jasmonic acid, ethylene and salicylic acid (SA) perception. Under challenging conditions, the level of resistance was higher than in non-challenging conditions; therefore, ISR is highly favourable and recommended for biological control of plant pathogenic diseases. *B. sphaericus* strain B43 was investigated for the induced resistance against *Globodera pallida* in potato roots by split root system. It was observed that, both living and heat-killed bacterial cell effectively reduced the incidence of *G. pallida* in potato roots [88]. It was reported that *B. pumilus* strain SE34 increased the level of SA in tobacco plant compared to non-treated plants [89].

Recently, it was demonstrated that microbial-originated volatiles have a role in elicitation of plant defence mechanism. The role of bacterial volatile for ISR elicitation was investigated by culturing bacteria and *Arabidopsis* seedlings on isolated edges of divided Petri dishes. *Arabidopsis* seedlings were continuously exposed to volatile compounds of *Bacillus* species for 4 days and a significant reduction in disease severity of soft rot was observed [90]. The chemical analysis of volatiles produced by the growth-promoting *B. subtilis* GB03 and *B. amyloliquefaciens* IN937a showed that their compositions are different from the non-growth-promoting bacterial strains DH5α. It was observed that the strains GB03 and IN937a released 2,3-butanediol and 3-hydroxy-2-butanone (acetoin) abundantly which were not observed for DH5α [91]. It was also shown that *B. subtilis* GB03-

originate volatile compounds that regulate ethylene biosynthesis enzymes, as well as ethylene biosynthesis-related genes (*ERF1*, *GST2*, and *CHIB*). It also regulated jasminic acid- and SA-mediated defence mechanism.

Enzymatic weapons

Besides production of antibiotics and elicitation of systemic resistance in plant against a variety of plant pathogenic diseases, *Bacillus* species are also capable of producing enzymes like chitinase and β-1,3-glucanase having a very strong lytic activity. These lytic enzymes synthesized by *Bacillus* species have proved to be very active in degrading fungal cell wall [92]. Studies conducted have shown that *Bacillus* species also produced many defence-related oxidative enzymes such as PPO, PO and PAL [93]. These oxidative enzymes induced lignin and oxidative phenolic compounds which play a role in contraction defence-related obstacle by producing structural changes in the cellular defence system against plant pathogens [94]. Podile and Laxmi [95] proved that PAL has an important role in the formation of lignin and flavonoid production. It also plays a key role in phenylpropanoid biosynthetic pathway. The defence-related activities of the enzymes have been proved in various plant species and against various plant pathogens [94].

An increase in PAL formation and activity was observed when it is exposed to the bacterial strain in comparison with untreated control [96]. Kang and Buchenauer [97] observed an enhancement in the phenolic activity in wheat crop induced by the resistance inducers against the powdery mildew. Phenolic compounds are highly effective against fungal plant pathogens, and hence play an important role in plant protection. Hahlbrock and Scheel [98] reported that PAL has a crucial role for phenolic compounds formation in plants through phenylpropanoid pathway. PPO also has a key role in plant defence elicitation against various plant pathogens. Li and Steffens [99] reported that the genetically modified tomato plants for enhanced production of PPO are found to be highly resistant against various pathogenic diseases. Thipyapong and Steffens [100] observed that PPO acts as catalyst in oxidative reactions of phenolic compounds. Many members of *Bacillus* species were found to be highly active in these types of defence-eliciting activities.

The basic goal of releasing hydrolase is to utilize the nutrient stored in substrate by converting it from unavailable form to available form. Moreover, bacteria release extracellular enzymes in combination with some other compounds to overcome the competition with other microbial agents. Most soils have sufficient amount of plant nutrients but present in insoluble form due to which plants are unable to uptake these nutrients for their normal growth [101]. β-1,3-Glucanases and chitinases actively contributed in defence of plant against a variety of plant pathogens while PO and PAL actively involved in phenylpropanoid breakdown in plant tissues [102].

Ramyabharathi et al. [103] studied the *B. subtilis* EPCO16 for the control of *F. oxysporum* f. sp. *lycopersici*. It was reported that the liquid and telic formulation of strain EPCO16 considerably elicited the defence-related enzymes and proteins (phenolics lyase, catalase and phenylalanine ammonia) in infected tomato plants. Liquid formulation significantly enhanced enzymatic activities in the tomato plant as well as in seed, seedling and soil treated with EPCO16. Spectrophotometric analysis of plants showed that the defensive proteins (phenolics, PAL and catalase) reached maximum levels at the seventh day of pathogen inoculation.

Chitinases and glucanases (laminarinase) fungal cell wall hydrolytic enzymes are produced by some hyperparasitic *Bacillus* species. Many strains of *B. subtilis* have been reported for their chitinolytic activities [104]. Podile and Prakash [105] reported the chitinolytic mechanism of *B. subtilis*. Chitin holds second position among the polysaccharides according to its abundance in nature. It is a β-1$\rightarrow$4-linked homopolymer of *N*-acetyl-d-glucosamine which is very important fungal cell wall strengthening element that offers rigidity to cell wall by hydrogen bonding between adjacent polymers. Thus, glycosidic bonds of constituting polysaccharides are the base for fungal cell wall integrity. Interference in these bonds deteriorates the cell wall and hence cell leakage. *Bacillus* species produced cell wall hydrolyzing enzymes (chitinases, glucanases and chitosanases) that efficiently hydrolyzed the cell wall of fungal pathogens. Therefore, these hydrolytic enzymes hold a great potential for the management of fungal pathogenic plant disease. As the plant cells lack chitin, chitinase application is more effective than glucanase [104]. Chitinase-producing bacteria supplemented with a chitinase substrate and 1% colloidal chitin considerably reduced the groundnut leaf spot disease [106,107].

B. amyloliquefaciens V656 synthesized two types of chitinases enzymes and both significantly inhibited *F. oxysporum* growth [108]. *B. subtilis* produced an antifungal chitinase enzyme with strong chitinitic activity against various pathogenic fungi [109]. *B. thuringiensis* inhibited *S. rolfsii* and various other pathogenic fungal diseases of soybean. Liu et al. showed that the chitinase from *B. thuringiensis* subsp. *colmeri* prevented the germination of fungal spores [110]. Bargabus et al. [111] investigated in their research that *B. mycoides* strain BacJ elicites systemic resistance in sugar beet which was

Table 2. Summary of *Bacillus*-induced systemic resistance principle eliciting factors and target pathogens.

Bacteria	Strain	Host plant	SIR eliciting factors	Target pathogen (s)	References
B. subtilus	174	Tomato	PAL, PPO and PO	*F. oxysporum*	[77]
B. subtilis	AUBS1	Rice	PAL and PO and PR proteins	*Oryza sativa* L.	[93]
B. subtilis	GB03	*Arabidopsis thaliana*	Ethylene biosynthesis enzymes	*Erwinia carotovora*	[122]
B. cereus	AR156	Loquat	PAL, PO, chitinase, β-1,3-glucanase, polyphenoloxidase and promoted accumulation of H_2O_2	*Colletotrichum acutatum*	[80]
B. subtilis	PTA-271	Grapevine	Lipoxygenase, PAL and chitinase	*Botrytis cinerea*	[123]
B. subtilis	B4	Cucumber	Indole acetic acid	*Colletotrichum orbiculare*	[124]
B. mycoides	Bac J	Sugar beet	Chitinase, β-1,3-glucanase and peroxidase	*Sercospora beticola*	[111]
B. subtilis	BBG111	Rice	Jasmonic acid (JA) and ethylene (ET) as well as abscisic acid (ABA) and auxin signalling	*R. solani*	[125]
B. subtilis	Bs16	Tomato	PPO and PO, PAL, chitinase and β-1,3-glucanase and accumulation of phenolics	*Alternaria solani*	[126]
B. subtilis	SE34 and GBO3	Rice	PO and PAL, PPO	*Xanthomonas oryzae* pv. oryzae	[127]
B. subtilis	OTPB1	Tomato	PO, PPO and superoxide dismutase	*Alternaria solani* and *Phytophthora infestans*	[56]
B. vallismortis	BS07	Chili pepper	Salicylic acid (SA)	*Phytophthora capsici* and *Colletotrichum acutatum,*	[24]
B. subtilis	GB03	Arabidopsis	Ethylene, 2,3-Butanediol	*Erwinia carotovora* subsp. carotovora	[90]
B. amyloliquefaciens	IN937a	Arabidopsis	Salicylic acid and jasmonic acid	*Erwinia carotovora* subsp. carotovora	[90]
B. pumilus	SE34	Pea	Phenolic compounds	*F. oxysporum* f. sp. pisi.	[83]

related with increased activity of PO and also enhanced the production of two ribozymes of β-1,3-glucanase and one isozyme of chitinase.

In nature, there is a diverse range of chitins presented with a diverse structure, and hence bacteria synthesize a variety of chitinases. According to amino acid sequence, chitinases are classified into 18, 19, and 20 glycosyl hydrolases. Family 18 of chitinolytic enzymes is multifarious and comprises chitinolytic enzymes from fungi, bacteria, viruses and some plants and animals. Type 19 chitinolytic enzymes comprise some *Streptomyces* and plant chitinases I, II, and IV [112] while type 20 consists of human, *Streptomycetes* and bacterial β-*N*-acetylhexosaminidases. Based on catalytic domains stature, bacterial chitinases are further classified in to A, B, and C groups [113]. *Bacillus licheniformis* synthesizes five chitinolytic enzymes (66, 62, 53, 49, and 42 kDa) while *B. circulans* synthesizes six different chitinases but only chitinase A1 is mainly involved in degradation of chitin. Chitin-binding protein (Cbp21) has a synergistic effect on β-chitin disruption [114].

Activities of these bacterial enzymes have been improved by the use of modern biotechnology. Homological-based enzymatic modelling played an important role in enhancing the activities of bacterial enzymes. Activity of β-galactosidase has been improved sixty six times while substrate activity was enhanced one-thousand times by DNA shuffling and screening [115]. Without any reduction in catalytic activity of phospholipase A1, its melting point increased by 7–10 °C by error-prone PCR and screening [116]. Thermal stability of Kanamycin nucleotidyl transferase increased up to 20 °C by DNA shuffling and screening/selection [117]. PCR-based site-directed mutagenesis was used to detect half-life of raw starch-digesting amylase (RSDA) by 20 folds [118]. Cellulose consumption of cellulase was increased three-fold through metabolic engineering [119].

The three-dimensional structure of catalytic domain showed that the tryptophan residues (W122 and W134) played a very important role in hydrolysis of chitin. Mutational studies represented that any change in these residues significantly reduced the catalytic activity of enzyme [120]. *Bacillus*-based chitinases vary with environmental conditions. Studies on macular diversity of bacterial-based chitinases showed that it is more diversified in arable soils. Phylogenetic data and multidimensional scaling (MDS) analysis of T-RFLP profiles revealed that the composition was considerably affected by the type of soil and pH [121]. Principle eliciting factors of systemic resistance and target pathogen are summarized in Table 2.

Colonization

Interspecies competition causes reduction in growth, productiveness and other activities of the competing organisms. Biological control arises when pathogenic and nonpathogenic organisms compete for space and nutrients around the host plant [1]. Plant and soil surface has a limited amount of nutrients. Therefore, for effective colonization of plant surface, pathogenic and nonpathogenic microbes must compete to fulfil their nutrient requirements. Plant exudates, senesced tissue or leachates are the main sources of nutrient supply on host

Table 3. Summary of important *Bacillus* strains in relation to colonization, their target pathogens and host plants.

Bacteria Species	Strain	Host plant	Target pathogen (s)	References
Bacillus spp.	B2-5	Ginseng	*Fusarium cf. incarnatum*	[129]
B. subtilis	HJ5	Cotton	*Verticillium dahliae* Kleb	[130]
B. subtilis	SQR9	Cucumber	*F. oxysporum*	[131]
B. subtilis	N11	Banana	*Fusarium* wilt	[133]
B. subtilis	B246	Avocado	*Dothiorella aromatic* and *Phomopsis perseae*	[134]
B. subtilis	M4	Cucumber	*Colletotrichum lagenarium* and *P. aphanidermatum*	[135]
B. subtilis	SB24	Tomato	*S. sclerotiorum*	[136]
B. subtilis	E1R-j	Wheat	*Ustilago tritici*	[137]
B. pumilus	SE34	Pea	*Fusarium oxysporum* f. sp. pisi	[83]
B. amyloliquefaciens	54	Watermelon	*Acidovorax avenae* subsp. citrulli	[65]
B. amyloliquefaciens	NBRISN13	Rice	Salt stress	[138]
B. amyloliquefacien	CM-2 and T-5	Tomato	*Ralstonia solanacearum*	[139]
B. subtilis	Lu144	Mulberry	*Ralstonia solanacearum*	[140]
B. megaterium	A6	Oilseed rape	*Sclerotinia sclerotiorum*	[141]
B. subtilis	QST 713	Tomato	*Fusarium*, *Pythium*, *Phytophthora*, *Rhizoctonia*, *Sclerotinia*, *Septoria*, and *Verticillium*	[142]
B. megaterium	B153-2-2	Soybean	*R. solani*	[143]
B. cereus	AR156	*Arabidopsis thaliana*	*Pseudomonas syringae*	[144]
B. amyloliquefaciens	HK34	Panax ginseng	*Phytophthora cactorum*	[85]
B. cereus	UW 85 and CF	Tobacco	*Phytophthora parasitica*	[145]

plant surface. It is difficult to demonstrate the direct role of competition in plant disease control but there are numerous indirect studies that have proved that pathogenic and nonpathogenic microbes compete for nutrients and space and thus play a very crucial role in pathogen severity and incidence reduction. In general, the soil-borne plant diseases (e.g. *Fusarium* and *Pythium* species) are more exposed to competition because they only infect through mycelial contact in comparison with those pathogenic diseases whose causal organisms directly germinate on plant surface and infect through infection peg and appressoria. Nonpathogenic microbes associated with photosphere protect plants by fast colonization and exhausting the developmental necessities thus makes them unavailable for pathogenic microbes.

Biocontrol can be established by competing for essential micronutrients, for example iron in rhizosphere, is extremely limited and its availability is highly dependent on soil. Iron is mostly in ferric form in oxidized and aerated soils which are water-insoluble at pH 7.4 and its concentration may be as low as 10^{-8} mol/L. This concentration is insufficient to support the growth and development of microorganisms. For survival under such situations, the microorganisms develop siderophores which enable the microbes to fulfil their iron requirement from the microenvironment. Kloepper and his coworkers [60] found out the role of siderophores for the biological management of *Erwinia carotovora* by several PGPR bacteria. The enhanced ability of beneficial nonpathogenic commercial microbes for utilization was suggested to be an important element for rapid colonization of rhizosphere and helpful for the shift of pathogenic microbes from the probable site of infection. Rapid colonization of tomato tissues by *Bacillus* species significantly reduced *Fusarium oxysporium* infection as well as the wilting index. For successful biological management of plant disease, colonization of plant tissues is considered as principle element, while for soil-borne diseases, root colonization by biological control agents has direct contribution [128]. A significant increase in colonization ability of *Bacillus* species was observed when pathogen (*Fusarium* cf. *incarnatum*) and biocontrol agent (*Bacillus* Isolate B2-5) were inoculated simultaneously on the ginseng tissues in comparison with separate inoculation [129]. *B. subtilis* strain HJ5 was tagged with a green fluorescent protein-encoding gene for easy investigation of its colonization ability. HJ5 successfully colonized the differentiating and elongating root tissues and bacterial population reached to its highest point (10^7) after three days of inoculation. Strain HJ5 significantly reduced the *Verticillium* wilt of cotton and apparent mechanism of this disease reduction was rapid colonization ability of strain HJ5 [130]. Zhang and coworkers [131] investigated the colonization of banana root by *B. subtilis* N11 under sand, hydroponic and natural soil systems and the results showed that the strain N11 efficiently colonized the banana roots under all of three culturing systems.

B. amyloliquefaciens strain C06 synthesized γ-polyglutamic acid and studies suggested that it played very important role in colonization of stain C06 and any interruption in the synthesis of γ-polyglutamic acid caused significant reduction in colonization ability of strain C06 [132]. Table 3 shows the important *Bacillus* strains in relation to colonization, their target pathogens and host plant.

Conclusion

Bacillus-based biological control agent delivers attractive, efficient and friendly method for the management of plant pests. The matters that demand considerations for the practical adoption of biological control agents

comprise the exposition of their mode of action, stability under field application, development of such formulation that can be used with other pesticides with synergetic effect and perfect demonstration of cost–benefit ratio for effective commercialization.

Bacillus species produce a variety of compounds that can be used for the management of a broad range of plant pests. Stable growth and development of biological agent under field conditions is still a problem due to adverse environmental conditions. Formulation of active product with perfect stabilizer that can optimize its activity under field conditions is an alternative and more effective strategy for the management of plant pest instead of using living bacteria directly. The bacterial-based formulated products, when used with other synthetic chemical pesticides, can be harmful for the living bacteria. The formulation that can enhance the shelf-life of bacterial product during storage, transportation and also during field application is also important. Proper knowledge and understanding of the bacterial active compound is necessary for a stable and efficient formulation.

Lipopeptides belong to a group of microbial-based peptides that enable the plant activation of defence mechanism. For biological control of plant pathogens *Bacillus*-originated lipopeptides play a very important role. Their unique physiochemical properties are mainly responsible for their effectiveness against a broad range of plant pathogens. Agitation of lipid bilayers, decline in surface tension and many other alterations in surface properties are the main qualities of these lipopeptides. Mass spectrometry is a rapid and efficient method for selection of effective strains of biological control of plant pathogens. Although recent advances have provided us some useful understanding of mechanism of lipopeptides with other interacting pathogens, studies mostly based on physiochemical activities and a broader view of the mechanisms are still missing.

Combined use of *Bacillus* species with different mechanism of action can enhance their effectiveness under greenhouse conditions. While combining the different groups, care must be taken so that each of them should have equal opportunity of colonization without any antagonistic effect among the biological control agents. Spore-forming ability and genetically engineered plants with *Bacillus* genes have been provided as an effective solution of many plant pathogenic diseases. The spore-forming property of *Bacillus* species gives them a prime importance in the field of biological control. This is because the spores produced by *Bacillus* species have the ability to endure the extreme environmental conditions. Therefore, attention should be put on the development of cost-effective and stable spores based products.

Diversity in *Bacillus* strains provides protection to plants in a variety of ways. Systemic-induced resistance and plant growth promotion play a principle role in biological plant protection. A large number of *Bacillus* strains have been developed for an effective control of plant pest and diseases. Most of the scientific investigations are made on signal transduction pathways in *Bacillus* species-treated plants. Biologically active microbes synthesize a variety of antimicrobial secondary metabolites but the exact measurement of active compound is difficult because of its low quantity in comparison with other ineffective compounds present on plant surface. The *Bacillus* species have the ability to produce compounds that belong to multiple classes of antibiotics which can be used for control of a broad range of plant pathogenic diseases.

For successful application of these biological agents, their ecological study is necessary. Definitely safety and worth of biological agents will be determined by its ecological success under field conditions. Practical understanding about the mode of action, diversity, ecological distribution and interacting environment into which the biological agents have to work will be valuable for successful adaptation of biological control for sustainable agricultural productivity.

Inaugurating the occurrence and functionality of biologically important microbes in a particular environment is the first step for understanding their nature and mode of action for controlling the pathogens under that environment. Due to the complexity of field conditions, extensive studies are required for fully understanding and characterizing the mode of action of these biological control agents.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

Ministry of Agriculture of the People's Republic of China [2013325].

ORCID

Jamil Shafi http://orcid.org/0000-0002-8670-6631

References

[1] Pal KK, Gardener BM. Biological control of plant pathogens. Plant Health Instruct. 2006;2:1117–1142.
[2] Barr PO, Soila P. Introduction of soft cannula into artery by direct percutaneous puncture. Observations on

technique and cannula materials. Angiology. 1960;11:168–172.
[3] Cook RJ, Weller DM, El-Banna AY, et al. Yield responses of direct-seeded wheat to rhizobacteria and fungicide seed treatments. Plant Dis. 2002;86(7):780–784.
[4] Cook RJ, Baker KF. The nature and practice of biological control of plant pathogens. St. Paul (MN): American Phytopathological Society; 1983.
[5] Verschuere L, Rombaut G, Sorgeloos P, et al. Probiotic bacteria as biological control agents in aquaculture. Microbiol Mol Biol Rev. 2000;64(4):655–671.
[6] Compant S, Duffy B, Nowak J, et al. Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. Appl Environ Microbiol. 2005;71(9):4951–4959.
[7] Denner W, Gillanders T. The legislative aspects of the use of industrial enzymes in the manufacture of food and food ingredients. In: Godfrey T, Reichelt J, editors. Industrial enzymology. New York: Stockton Press; 1996. p. 397–412.
[8] Nemutanzhela ME, Roets Y, Gardiner N, et al. The use and benefits of *Bacillus* based biological agents in aquaculture. In: Hernández-Vergara MP, Pérez-Rostro CI, editors. Sustainable aquaculture techniques. Rijeka (Croatia): INTECH; 2014. p. 33.
[9] Cavaglieri L, Orlando J, Etcheverry M. In vitro influence of bacterial mixtures on *Fusarium verticillioides* growth and fumonisin B1 production: effect of seeds treatment on maize root colonization. Lett Appl Microbiol. 2005;41(5):390–396.
[10] Microbiology UDoPa. Antimicrob Pept database. 2016; 18 April. Available from: http://aps.unmc.edu/AP/main.php
[11] Zhao X, Zhou Z-j, Han Y, et al. Isolation and identification of antifungal peptides from *Bacillus* BH072, a novel bacterium isolated from honey. Microbiol Res. 2013;168(9):598–606.
[12] Gong A-D, Li H-P, Yuan Q-S, et al. Antagonistic Mechanism of Iturin A and Plipastatin A from *Bacillus amyloliquefaciens* S76-3 from wheat spikes against *Fusarium graminearum*. PLoS One. 2015;10(2):e0116871.
[13] Maget-Dana R, Ptak M, Peypoux F, et al. Pore-forming properties of iturin A, a lipopeptide antibiotic. Biochim Biophys. 1985;815(3):405–409.
[14] Hirata F, Axelrod J. Phospholipid methylation and biological signal transmission. Science. 1980;209(4461):1082–1090.
[15] Vadas P, Pruzanski W, Kim J, et al. The proinflammatory effect of intra-articular injection of soluble human and venom phospholipase A2. Am J Med Sci. 1989;134(4):807.
[16] Nishikiori T, Naganawa H, Muraoka Y, et al. Plipastatins: new inhibitors of phospholipase A2, produced by *Bacillus cereus* BMG302-fF67. III. Structural elucidation of plipastatins. J Antibiot. 1986;39(6):755–761.
[17] Volpon L, Besson FLancelin J-M. NMR structure of antibiotics plipastatins A and B from *Bacillus subtilis* inhibitors of phospholipase A 2. FEBS Lett. 2000;485(1):76–80.
[18] Thasana N, Prapagdee B, Rangkadilok N, et al. *Bacillus subtilis* SSE4 produces subtulene A, a new lipopeptide antibiotic possessing an unusual C15 unsaturated β-amino acid. FEBS Lett. 2010;584(14):3209–3214.
[19] Ohno A, Ano T, Shoda M. Effect of temperature on production of lipopeptide antibiotics, iturin A and surfactin by a dual producer, *Bacillus subtilis* RB14, in solid-state fermentation. J Ferment Bioeng. 1995;80(5):517–519.
[20] YE Y-F, LI Q-Q, Gang F, et al. Identification of antifungal substance (Iturin A 2) produced by *Bacillus subtilis* B47 and its effect on southern corn leaf blight. J Integr Agric. 2012;11(1):90–99.
[21] Xu D, Wang Y, Sun L, et al. Inhibitory activity of a novel antibacterial peptide AMPNT-6 from *Bacillus subtilis* against *Vibrio parahaemolyticus* in shrimp. Food Control. 2013;30(1):58–61.
[22] Gong Q, Zhang C, Lu F, et al. Identification of bacillomycin D from *Bacillus subtilis* fmbJ and its inhibition effects against *Aspergillus flavus*. Food Control. 2014;36(1):8–14.
[23] Dunlap CA, Bowman MJ, Schisler DA. Genomic analysis and secondary metabolite production in *Bacillus amyloliquefaciens* AS 43.3: a biocontrol antagonist of *Fusarium* head blight. Biol Control. 2013;64(2):166–175.
[24] Park J-W, Balaraju K, Kim J-W, et al. Systemic resistance and growth promotion of chili pepper induced by an antibiotic producing *Bacillus vallismortis* strain BS07. Biol Control. 2013;65(2):246–257.
[25] Qi G, Zhu F, Du P, et al. Lipopeptide induces apoptosis in fungal cells by a mitochondria-dependent pathway. Peptides. 2010;31(11):1978–1986.
[26] Cao Y, Xu Z, Ling N, et al. Isolation and identification of lipopeptides produced by B. *subtilis* SQR 9 for suppressing *Fusarium* wilt of cucumber. Sci Hortic. 2012;135:32–39.
[27] Baysal Ö, Çalışkan M Yeşilova Ö. An inhibitory effect of a new *Bacillus subtilis* strain (EU07) against *Fusarium oxysporum* f. sp. radicis-lycopersici. Physiol Mol Plant Pathol. 2008;73(1):25–32.
[28] Chen H, Wang L, Su C, et al. Isolation and characterization of lipopeptide antibiotics produced by *Bacillus subtilis*. Lett Appl Microbiol. 2008;47(3): 180–186.
[29] Wu S, Jia S, Sun D, et al. Purification and characterization of two novel antimicrobial peptides subpeptin JM4-A and subpeptin JM4-B produced by *Bacillus subtilis* JM4. Curr Microbiol. 2005;51(5):292–296.
[30] Huang C-J, Wang T-K, Chung S-C, et al. Identification of an antifungal chitinase from a potential biocontrol agent, *Bacillus cereus* 28-9. BMB Rep. 2005;38(1):82–88.
[31] Liu Y, Chen Z, Ng T, et al. Bacisubin, an antifungal protein with ribonuclease and hemagglutinating activities from *Bacillus subtilis* strain B-916. Peptides. 2007;28(3):553–559.
[32] Li J, Yang Q, Zhao L-H, et al. Purification and characterization of a novel antifungal protein from *Bacillus subtilis* strain B29. J Zhejiang Univ Sci B. 2009;10(4):264–272.
[33] Xie J, Zhang R, Shang C, et al. Isolation and characterization of a bacteriocin produced by an isolated *Bacillus subtilis* LFB112 that exhibits antimicrobial activity against domestic animal pathogens. Afr J Biotechnol. 2009;8(20):5611–5619.
[34] Kim PI, Ryu J, Kim YH, et al. Production of biosurfactant lipopeptides Iturin A, fengycin and surfactin A from *Bacillus subtilis* CMB32 for control of *Colletotrichum gloeosporioides*. J Microbiol Biotechnol. 2010;20(1):138–145.
[35] Fuchs SW, Jaskolla TW, Bochmann S, et al. Entianin, a novel subtilin-like lantibiotic from *Bacillus subtilis* subsp. spizizenii DSM 15029T with high antimicrobial activity. Appl Environ Microbiol. 2011;77(5):1698–1707.

[36] Yeo I-C, Lee NK, Cha C-J, et al. Narrow antagonistic activity of antimicrobial peptide from *Bacillus subtilis* SCK-2 against Bacillus cereus. J Biosci Bioeng. 2011;112(4):338–344.
[37] Hammami I, Jaouadi B, Bacha AB, et al. *Bacillus subtilis* bacteriocin Bac 14B with a broad inhibitory spectrum: purification, amino acid sequence analysis, and physicochemical characterization. Biotechnol Bioprocess Eng. 2012;17(1):41–49.
[38] Vanittanakom N, Loeffler W, Koch U, et al. Fengycin-A novel antifungal lipopeptide antibiotic produced by *Bacillus subtilis* F-29-3. J Antibiot (Tokyo). 1986;39(7):888–901.
[39] Abdel−Mohsein HS, Sasaki T, Tada C, et al. Characterization and partial purification of a bacteriocin−like substance produced by thermophilic *Bacillus licheniformis* H1 isolated from cow manure compost. Anim J Sci. 2011;82(2):340–351.
[40] Kamoun F, Mejdoub H, Aouissaoui H, et al. Purification, amino acid sequence and characterization of Bacthuricin F4, a new bacteriocin produced by *Bacillus thuringiensis*. J Appl Microbiol. 2005;98(4):881–888.
[41] Roy A, Mahata D, Paul D, et al. Purification, biochemical characterization and self-assembled structure of a fengycin-like antifungal peptide from *Bacillus thuringiensis* strain SM1. Front Microbiol. 2013;4:1–6.
[42] Serpil U, Kati H. Purification and characterization of the bacteriocin thuricin Bn1 produced by *Bacillus thuringiensis* subsp. kurstaki Bn1 isolated from a hazelnut pest. J Microbiol Biotechnol. 2013;23(2):167–176.
[43] Benitez LB, Velho RV, Lisboa MP, et al. Isolation and characterization of antifungal peptides produced by *Bacillus amyloliquefaciens* LBM5006. J Microbiol. 2010;48(6):791–797.
[44] Halimi B, Dortu C, Arguelles-Arias A, et al. Antilisterial activity on poultry meat of amylolysin, a bacteriocin from *Bacillus amyloliquefaciens* GA1. Probiotics Antimicrob Proteins. 2010;2(2):120–125.
[45] Scholz R, Molohon KJ, Nachtigall J, et al. Plantazolicin, a novel microcin B17/streptolysin S-like natural product from *Bacillus amyloliquefaciens* FZB42. J Bacteriol. 2011;193(1):215–224.
[46] Kavitha S, Senthilkumar S, Gnanamanickam S, et al. Isolation and partial characterization of antifungal protein from *Bacillus polymyxa* strain VLB16. Process Biochem. 2005;40(10):3236–3243.
[47] Awais M, Shah AA, Hameed A, et al. Isolation, identification and optimization of bacitracin produced by *Bacillus* sp. Pak J Zool. 2007;39(4):1303.
[48] Zhao Z, Wang Q, Wang K, et al. Study of the antifungal activity of *Bacillus vallismortis* ZZ185 in vitro and identification of its antifungal components. Bioresour Technol. 2010;101(1):292–297.
[49] Lawton EM, Cotter PD, Hill C, et al. Identification of a novel two-peptide lantibiotic, haloduracin, produced by the alkaliphile *Bacillus halodurans* C-125. FEMS Microbiol Lett. 2007;267(1):64–71.
[50] Ayed HB, Hmidet N, Béchet M, et al. Identification and biochemical characteristics of lipopeptides from *Bacillus mojavensis* A21. Process Biochem. 2014;49(10):1699–1707.
[51] Chopra L, Singh G, Choudhary V, et al. Sonorensin: an antimicrobial peptide, belonging to the heterocycloanthracin subfamily of bacteriocins, from a new marine isolate, *Bacillus sonorensis* MT93. Appl Environ Microbiol. 2014;80(10):2981–2990.
[52] Riazi S, Wirawan R, Badmaev V, et al. Characterization of lactosporin, a novel antimicrobial protein produced by *Bacillus coagulans* ATCC 7050. J Appl Microbiol. 2009;106(4):1370–1377.
[53] Romero D, de Vicente A, Rakotoaly RH, et al. The iturin and fengycin families of lipopeptides are key factors in antagonism of *Bacillus subtilis* toward *Podosphaera fusca*. Mol Plant-Microbe Interact. 2007;20(4):430–440.
[54] Chen XH, Koumoutsi A, Scholz R, et al. Comparative analysis of the complete genome sequence of the plant growth-promoting bacterium *Bacillus amyloliquefaciens* FZB42. Nat Biotechnol. 2007;25(9):1007–1014.
[55] Harman GE. Multifunctional fungal plant symbionts: new tools to enhance plant growth and productivity. New Phytol. 2011;189(3):647–649.
[56] Chowdappa P, Kumar SM, Lakshmi MJ, et al. Growth stimulation and induction of systemic resistance in tomato against early and late blight by *Bacillus subtilis* OTPB1 or *Trichoderma harzianum* OTPB3. Biol Control. 2013;65(1):109–117.
[57] Idris EE, Iglesias DJ, Talon M, et al. Tryptophan-dependent production of indole-3-acetic acid (IAA) affects level of plant growth promotion by *Bacillus amyloliquefaciens* FZB42. Mol Plant-Microbe Interact. 2007;20(6):619–626.
[58] Gravel V, Antoun H, Tweddell RJ. Growth stimulation and fruit yield improvement of greenhouse tomato plants by inoculation with *Pseudomonas putida* or *Trichoderma atroviride*: possible role of indole acetic acid (IAA). Soil Biol Biochem. 2007;39(8):1968–1977.
[59] Shoresh M, Harman GE, Mastouri F. Induced systemic resistance and plant responses to fungal biocontrol agents. Annu Rev Phytopathol. 2010;48:21–43.
[60] Kloepper JW, Ryu C-M, Zhang S. Induced systemic resistance and promotion of plant growth by *Bacillus spp*. Phytopathology. 2004;94(11):1259–1266.
[61] Gardner G. Plant hormone signaling. HortScience. 2009;44(1):222–223.
[62] Srivastava LM. Plant growth and development: hormones and environment. San Diego (CA): Academic press; 2002.
[63] Vessey JK. Plant growth promoting rhizobacteria as biofertilizers. Plant Soil. 2003;255(2):571–586.
[64] Ghanashyam C, Jain M. Role of auxin-responsive genes in biotic stress responses. Plant Signal Behav. 2009;4(9):846–848.
[65] Jiang C-H, Wu F, Yu Z-Y, et al. Study on screening and antagonistic mechanisms of *Bacillus amyloliquefaciens* 54 against bacterial fruit blotch (BFB) caused by *Acidovorax avenae* subsp. *citrulli*. Microbiol Res. 2015;170:95–104.
[66] Ramesh A, Sharma SK, Sharma MP, et al. Inoculation of zinc solubilizing *Bacillus aryabhattai* strains for improved growth, mobilization and biofortification of zinc in soybean and wheat cultivated in vertisols of central India. Appl Soil Ecol. 2014;73:87–96.
[67] Hong SH, Lee EY. Vegetation restoration and prevention of coastal sand dunes erosion using ion exchange resins and the plant growth-promoting rhizobacteria *Bacillus* sp. SH1RP8 isolated from indigenous plants. Int Biodeterior Biodegrad. 2014;95:262–269.

[68] Lin Y, Du D, Si C, et al. Potential biocontrol *Bacillus* sp. strains isolated by an improved method from vinegar waste compost exhibit antibiosis against fungal pathogens and promote growth of cucumbers. Biol Control. 2014;71:7–15.
[69] Wei X, Yan P-S, Wu H-Q, et al. Antagonizing *Aspergillus parasiticus* and promoting peanut growth of *Bacillus* isolated from peanut geocarposphere soil. J Integr Agric. 2014;13(11):2445–2451.
[70] Nain L, Yadav R, Saxena J. Characterization of multifaceted *Bacillus* sp. RM-2 for its use as plant growth promoting bioinoculant for crops grown in semi arid deserts. Appl Soil Ecol. 2012;59:124–135.
[71] López-Valdez F, Fernández-Luqueno F, Ceballos-Ramírez J, et al. A strain of *Bacillus subtilis* stimulates sunflower growth (*Helianthus annuus* L.) temporarily. Sci Hortic. 2011;128(4):499–505.
[72] Durrant W Dong X. Systemic acquired resistance. Annu Rev Phytopathol. 2004;42:185–209.
[73] Van Loon L, Bakker P, Pieterse C. Systemic resistance induced by rhizosphere bacteria. Annu Rev Phytopathol. 1998;36(1):453–483.
[74] Van Wees SC, Van der Ent S, Pieterse CM. Plant immune responses triggered by beneficial microbes. Curr Opin Plant Biol. 2008;11(4):443–448.
[75] Park K, Paul D, Kim YK, et al. Induced systemic resistance by *Bacillus vallismortis* EXTN-1 suppressed bacterial wilt in tomato caused by *Ralstonia solanacearum*. Plant Pathol J. 2007;23(1):22.
[76] Park K, Ahn I-P, Kim C-H. Systemic resistance and expression of the pathogenesis-related genes mediated by the plant growth-promoting rhizobacterium *Bacillus amyloliquefaciens* EXTN-1 against anthracnose disease in cucumber. Mycobiology. 2001;29 (1):48–53.
[77] Akram W, Anjum T. Quantitative changes in defense system of tomato induced by two strains of *Bacillus* against *Fusarium* wilt. Indian J Fund Appl Life Sci. 2011;1:7–13.
[78] Gupta V, Bochow H, Dolej S, et al. Ein das Pflanzenwachstum fördernder *Bacillus subtilis*-Stamm als potentieller Resistenzinduktor gegen die *Fusarium*-Welke an Tomaten [Plant growth-promoting *Bacillus subtilis* strain as potential inducer of systemic resistance in tomato against *Fusarium* wilt]. J Plant Dis Prot. 2000;145–154.
[79] Jayaraj J, Anand A, Muthukrishnan S. Pathogenesis-related proteins and their roles in resistance to fungal pathogens. In: Punja ZK, editor. Fungal disease resistance in pants: biochemistry, molecular biology, and genetic engineering. New York: Haworth Press. 2004; p. 139–177.
[80] Wang X, Wang L, Wang J, et al. *Bacillus cereus* AR156-induced resistance to *Colletotrichum acutatum* is associated with priming of defense responses in loquat fruit. PloS One. 2014;9(11):e112494.
[81] Ahn I-P, Park K, Kim C-H. Rhizobacteria-induced resistance perturbs viral disease progress and triggers defense-related gene expression. Mol Cells. 2002;13 (2):302–308.
[82] Guo J-H, Qi H-Y, Guo Y-H, et al. Biocontrol of tomato wilt by plant growth-promoting rhizobacteria. Biol Control. 2004;29(1):66–72.
[83] Benhamou N, Kloepper JW, Quadt-Hallman A, et al. Induction of defense-related ultrastructural modifications in pea root tissues inoculated with endophytic bacteria. Plant Physiol. 1996;112(3):919–929.
[84] Benhamou N, Kloepper JW, Tuzun S. Induction of resistance against *Fusarium* wilt of tomato by combination of chitosan with an endophytic bacterial strain: ultrastructure and cytochemistry of the host response. Planta. 1998;204(2):153–168.
[85] Lee BD, Dutta S, Ryu H, et al. Induction of systemic resistance in Panax ginseng against *Phytophthora cactorum* by native *Bacillus amyloliquefaciens* HK34. J Ginseng Res. 2015;39(3):213–220.
[86] Jetiyanon K, Fowler WD, Kloepper JW. Broad-spectrum protection against several pathogens by PGPR mixtures under field conditions in Thailand. Plant Dis. 2003;87 (11):1390–1394.
[87] Van Loon L, Bakker P. Induced systemic resistance as a mechanism of disease suppression by rhizobacteria, in PGPR: biocontrol and biofertilization. Dordrecht (Netherlands): Springer; 2006. p. 39–66.
[88] Hasky-Günther K, Hoffmann-Hergarten S, Sikora RA. Resistance against the potato cyst nematode *Globodera pallida* systemically induced by the rhizobacteria *Agrobacterium radiobacter* (G12) and *Bacillus sphaericus* (B43). Fundam Appl Nematol. 1998;21(5):511–517.
[89] Zhang S, Moyne A-L, Reddy M, et al. The role of salicylic acid in induced systemic resistance elicited by plant growth-promoting rhizobacteria against blue mold of tobacco. Biol Control. 2002;25(3):288–296.
[90] Ryu C-M, Farag MA, Hu C-H, et al. Bacterial volatiles induce systemic resistance in *Arabidopsis*. Plant Physiol. 2004;134(3):1017–1026.
[91] Ryu CM, Hu CH, Reddy M, et al. Different signaling pathways of induced resistance by rhizobacteria in *Arabidopsis thaliana* against two pathovars of *Pseudomonas syringae*. New Phytol. 2003;160(2):413–420.
[92] Leelasuphakul W, Sivanunsakul P, Phongpaichit S. Purification, characterization and synergistic activity of β-1,3-glucanase and antibiotic extract from an antagonistic *Bacillus subtilis* NSRS 89-24 against rice blast and sheath blight. Enzyme Microb Technol. 2006;38(7):990–997.
[93] Jayaraj J, Yi H, Liang G, et al. Blattapplikation von *Bacillus subtilis* AUBS1 reduziert die Blattscheidendürre und induziert Abwehrmechanismen in Reis [Foliar application of *Bacillus subtilis* AUBS1 reduces sheath blight and triggers defense mechanisms in rice]. J Plant Dis Prot. 2004;111(2):115–125.
[94] Thilagavathi R, Saravanakumar D, Ragupathi N, et al. A combination of biocontrol agents improves the management of dry root rot (*Macrophomina phaseolina*) in greengram. Phytopathol Mediterr. 2007;46(2):157–167.
[95] Sailaja P, Podile A, Reddanna P. Biocontrol strain of *Bacillus subtilis* AF 1 rapidly induces lipoxygenase in groundnut (*Arachis hypogaea* L.) compared to crown rot pathogen *Aspergillus niger*. Eur J Plant Pathol. 1998;104 (2):125–132.
[96] Arfaoui A, El Hadrami A, Mabrouk Y, et al. Treatment of chickpea with *Rhizobium* isolates enhances the expression of phenylpropanoid defense-related genes in response to infection by *Fusarium oxysporum* f. sp. ciceris. Plant Physiol Biochem. 2007;45(6):470–479.
[97] Kang Z, Buchenauer H. Ultrastructural and immunocytochemical investigation of pathogen development and

host responses in resistant and susceptible wheat spikes infected by *Fusarium culmorum*. Physiol Mol Plant Pathol. 2000;57(6):255–268.
[98] Hahlbrock K, Scheel D. Physiology and molecular biology of phenylpropanoid metabolism. Annu Rev Plant Biol. 1989;40(1):347–369.
[99] Li L, Steffens JC. Overexpression of polyphenol oxidase in transgenic tomato plants results in enhanced bacterial disease resistance. Planta. 2002;215(2):239–247.
[100] Thipyapong P, Steffens JC. Tomato polyphenol oxidase (differential response of the polyphenol oxidase F promoter to injuries and wound signals). Plant Physiol. 1997;115(2):409–418.
[101] Francis I, Holsters M, Vereecke D. The Gram−positive side of plant–microbe interactions. Environ Microbiol. 2010;12(1):1–12.
[102] Vidhyasekaran P, Kamala N, Ramanathan A, et al. Induction of systemic resistance by *Pseudomonas fluorescens* Pf1 against *Xanthomonas oryzae* pv. Oryzae in rice leaves. Phytoparasitica. 2001;29(2):155–166.
[103] Ramyabharathi S, Meena B, Raguchander T. Induction of chitinase and β-1,3-glucanase PR proteins in tomato through liquid formulated *Bacillus subtilis* EPCO 16 against *Fusarium* wilt. J Today Biol Sci: Res Rev. 2012;1(1):50–60.
[104] Das SN, Dutta S, Kondreddy A, et al. Plant growth-promoting chitinolytic *Paenibacillus elgii* responds positively to tobacco root exudates. J Plant Growth Regul. 2010;29 (4):409–418.
[105] Podile A, Prakash A. Lysis and biological control of *Aspergillus niger* by *Bacillus subtilis* AF 1. Can J Microbiol. 1996;42(6):533–538.
[106] Kishore G, Pande S. Chitin−supplemented foliar application of chitinolytic *Bacillus cereus* reduces severity of Botrytis gray mold disease in chickpea under controlled conditions. Lett Appl Microbiol. 2007;44(1):98–105.
[107] Huang X, Lu Z, Bie X, et al. Optimization of inactivation of endospores of *Bacillus cereus* by antimicrobial lipopeptides from *Bacillus subtilis* fmbj strains using a response surface method. Appl Microbiol Biotechnol. 2007;74(2):454–461.
[108] Wang J, Liu J, Wang X, et al. Application of electrospray ionization mass spectrometry in rapid typing of fengycin homologues produced by *Bacillus subtilis*. Lett Appl Microbiol. 2004;39(1):98–102.
[109] Chang X, Alderson PG, Wright CJ. Enhanced UV-B radiation alters basil (*Ocimum basilicum* L.) growth and stimulates the synthesis of volatile oils. J Hortic For. 2009;1 (2):027–031.
[110] Liu X-Y, Ruan L-F, Hu Z-F, et al. Genome-wide screening reveals the genetic determinants of an antibiotic insecticide in *Bacillus thuringiensis*. J Biol Chem. 2010;285 (50):39191–39200.
[111] Bargabus R, Zidack N, Sherwood J, et al. Characterisation of systemic resistance in sugar beet elicited by a non-pathogenic, phyllosphere-colonizing *Bacillus mycoides*, biological control agent. Physiol Mol Plant Pathol. 2002;61(5):289–298.
[112] Hart AC, Sims S, Kaplan JM. Synaptic code for sensory modalities revealed by *C. elegans* GLR-1 glutamate receptor. Nature. 1995;378(6552):82–85.
[113] Watanabe Y, Yamaguchi M, Sakamoto J, et al. Characterization of plasma membrane H+−ATPase from salt−tolerant yeast *Candida versatilis*. Yeast. 1993;9(3):213–220.
[114] Ruiz-Sánchez R, Blake R, Castro-Gámez H, et al. Short communication: changes in the association between milk yield and age at first calving in Holstein cows with herd environment level for milk yield. J Dairy Sci. 2007;90(10):4830–4834.
[115] Zhang F, Dashti N, Hynes R, et al. Plant growth-promoting rhizobacteria and soybean [*Glycine max* (L.) Merr.] growth and physiology at suboptimal root zone temperatures. Ann Bot. 1997; 79(3):243–249.
[116] Hoang L, Song KS, Rhee IK, et al. Mechanism by which *Bacillus*-derived 2-aminobenzoic acid inhibits the growth of *Arabidopsis thaliana* roots. J. Plant Biol. 2007;50(4): 514–516.
[117] Hoseki J, Yano T, Koyama Y, et al. Directed evolution of thermostable kanamycin-resistance gene: a convenient selection marker for *Thermus thermophilus*. J Biochem. 1999;126(5):951–956.
[118] Shiau R-J, Hung H-C, Jeang C-L. Improving the thermostability of raw-starch-digesting amylase from a *Cytophaga* sp. by site-directed mutagenesis. Appl Environ Microbiol. 2003;69(4):2383–2385.
[119] Guedon E, Desvaux M, Petitdemange H. Improvement of cellulolytic properties of *Clostridium cellulolyticum* by metabolic engineering. Appl Environ Microbiol. 2002;68 (1):53–58.
[120] Kim KK, Kang JG, Moon SS, et al. Isolation and identification of antifungal N-butylbenzenesulphonamide produced by *Pseudomonas* sp. AB2. J Antibiot (Tokyo). 2000;53(2):131–136.
[121] Terahara T, Ikeda S, Noritake C, et al. Molecular diversity of bacterial chitinases in arable soils and the effects of environmental factors on the chitinolytic bacterial community. Soil Biol Biochem. 2009;41(3):473–480.
[122] Kwon YS, Ryu C-M, Lee S, et al. Proteome analysis of *Arabidopsis* seedlings exposed to bacterial volatiles. Planta. 2010;232(6):1355–1370.
[123] Trotel-Aziz P, Couderchet M, Biagianti S, et al. Characterization of new bacterial biocontrol agents *Acinetobacter*, *Bacillus*, *Pantoea* and *Pseudomonas* spp. mediating grapevine resistance against *Botrytis cinerea*. Environ Exp Bot. 2008;64(1):21–32.
[124] Park K, Park J-W, Lee S-W, et al. Disease suppression and growth promotion in cucumbers induced by integrating PGPR agent *Bacillus subtilis* strain B4 and chemical elicitor ASM. Crop Protect. 2013;54:199–205.
[125] Chandler S, Van Hese N, Coutte F, et al. Role of cyclic lipopeptides produced by *Bacillus subtilis* in mounting induced immunity in rice (*Oryza sativa* L.). Physiol Mol Plant Pathol. 2015;91:20–30.
[126] Latha P, Anand T, Ragupathi N, et al. Antimicrobial activity of plant extracts and induction of systemic resistance in tomato plants by mixtures of PGPR strains and Zimmu leaf extract against *Alternaria solani*. Biol Control. 2009;50(2):85–93.
[127] Udayashankar A, Nayaka SC, Reddy M, et al. Plant growth-promoting rhizobacteria mediate induced systemic resistance in rice against bacterial leaf blight caused by *Xanthomonas oryzae* pv. *oryzae*. Biol Control. 2011;59(2):114–122.
[128] Cavaglieri L, Orlando J, Rodriguez M, et al. Biocontrol of *Bacillus subtilis* against *Fusarium verticillioides* in vitro and at the maize root level. Res Microbiol. 2005;156(5):748–754.

[129] Song M, Yun HY, Kim YH. Antagonistic *Bacillus* species as a biological control of ginseng root rot caused by *Fusarium* cf. *incarnatum*. J Ginseng Res. 2014;38(2):136–145.
[130] Li S, Zhang N, Zhang Z, et al. Antagonist *Bacillus subtilis* HJ5 controls *Verticillium* wilt of cotton by root colonization and biofilm formation. Biol Fertil Soils. 2013;49 (3):295–303.
[131] Cao Y, Zhang Z, Ling N, et al. *Bacillus subtilis* SQR 9 can control *Fusarium* wilt in cucumber by colonizing plant roots. Biol Fertil Soils. 2011;47(5):495–506.
[132] Liu J, He D, Li X-z, et al. γ-Polyglutamic acid (γ-PGA) produced by *Bacillus amyloliquefaciens* C06 promoting its colonization on fruit surface. Int J Food Microbiol. 2010;142(1):190–197.
[133] Zhang N, Wu K, He X, et al. A new bioorganic fertilizer can effectively control banana wilt by strong colonization with *Bacillus subtilis* N11. Plant Soil. 2011;344(1–2):87–97.
[134] Demoz BT, Korsten L. *Bacillus subtilis* attachment, colonization, and survival on avocado flowers and its mode of action on stem-end rot pathogens. Biol Control. 2006;37 (1):68–74.
[135] Ongena M, Duby F, Rossignol F, et al. Stimulation of the lipoxygenase pathway is associated with systemic resistance induced in bean by a nonpathogenic *Pseudomonas* strain. Mol Plant-Microbe Interact. 2004;17(9):1009–1018.
[136] Clayton MK, Hudelson BD. Analysis of spatial patterns in the phyllosphere. In: Andrews JH, Hirano SS, editors. Microbial ecology of leaves. New York: Springer; 1991. p. 111–131.
[137] Baker CJ, Stavely J, Thomas C, et al. Inhibitory effect of *Bacillus subtilis* on *Uromyces phaseoli* and on development of rust pustules on bean leaves. Phytopathology. 1983;73(8):1148–1152.
[138] Nautiyal CS, Srivastava S, Chauhan PS, et al. Plant growth-promoting bacteria *Bacillus* amyloliquefaciens NBRISN13 modulates gene expression profile of leaf and rhizosphere community in rice during salt stress. Plant Physiol Biochem. 2013;66:1–9.
[139] Tong-Jian X, Fang C, Chao G, et al. *Bacillus cereus* X5 enhanced bio-organic fertilizers effectively control root-knot nematodes (*Meloidogyne* sp.). Pedosphere. 2013;23 (2):160–168.
[140] Ji X, Lu G, Gai Y, et al. Biological control against bacterial wilt and colonization of mulberry by an endophytic *Bacillus subtilis* strain. FEMS Microbiol Ecol. 2008;65(3):565–573.
[141] Hu X, Roberts DP, Xie L, et al. *Bacillus megaterium* A6 suppresses *Sclerotinia sclerotiorum* on oilseed rape in the field and promotes oilseed rape growth. Crop Protect. 2013;52:151–158.
[142] Kinsella K, Schulthess CP, Morris TF, et al. Rapid quantification of *Bacillus subtilis* antibiotics in the rhizosphere. Soil Biol Biochem. 2009;41(2):374–379.
[143] Zheng X, Sinclair J. The effects of traits of *Bacillus megaterium* onseed and root colonization and their correlation with the suppression of *Rhizoctonia* root rot of soybean. BioControl. 2000;45(2):223–243.
[144] Paul Chowdhury S, Uhl J, Grosch R, et al. Cyclic lipopeptides of *Bacillus amyloliquefaciens* subsp. plantarum colonizing the lettuce rhizosphere enhance plant defence responses towards the bottom rot pathogen *Rhizoctonia solani*. Mol Plant-Microbe Interact. 2015;28(9):984–995.
[145] Blagoeva-Nikolaeva V, Slavov S, Varsano L. Possibilities for biological control of black-shank disease in tobacco with *Bacillus cereus*. Biotechnol Biotechnol Equip. 1995;9 (1):36–39.