Review

The Significance of *Bacillus* spp. in Disease Suppression and Growth Promotion of Field and Vegetable Crops

Dragana Miljaković [1],* , Jelena Marinković [1] and Svetlana Balešević-Tubić [2]

1 Department of Microbiological Preparations, Institute of Field and Vegetable Crops, Maksima Gorkog 30, 21000 Novi Sad, Serbia; jelena.marinkovic@ifvcns.ns.ac.rs
2 Soybean Department, Institute of Field and Vegetable Crops, Maksima Gorkog 30, 21000 Novi Sad, Serbia; svetlana.tubic@ifvcns.ns.ac.rs
* Correspondence: dragana.bjelic@ifvcns.ns.ac.rs

check for updates

Abstract: *Bacillus* spp. produce a variety of compounds involved in the biocontrol of plant pathogens and promotion of plant growth, which makes them potential candidates for most agricultural and biotechnological applications. Bacilli exhibit antagonistic activity by excreting extracellular metabolites such as antibiotics, cell wall hydrolases, and siderophores. Additionally, *Bacillus* spp. improve plant response to pathogen attack by triggering induced systemic resistance (ISR). Besides being the most promising biocontrol agents, *Bacillus* spp. promote plant growth via nitrogen fixation, phosphate solubilization, and phytohormone production. Antagonistic and plant growth-promoting strains of *Bacillus* spp. might be useful in formulating new preparations. Numerous studies of a wide range of plant species revealed a steady increase in the number of *Bacillus* spp. identified as potential biocontrol agents and plant growth promoters. Among different mechanisms of action, it remains unclear which individual or combined traits could be used as predictors in the selection of the best strains for crop productivity improvement. Due to numerous factors that influence the successful application of *Bacillus* spp., it is necessary to understand how different strains function in biological control and plant growth promotion, and distinctly define the factors that contribute to their more efficient use in the field.

Keywords: *Bacillus*; biocontrol agents; antibiotics; lytic enzymes; siderophores; induced systemic resistance; plant growth-promoting rhizobacteria

1. Introduction

Plant diseases, caused by various microorganisms, including fungi, bacteria, viruses, nematodes and protozoa, affect agricultural production and result in major yield losses [1]. Approximately 20–40% of losses in crop yield are caused by pathogenic infections [2]. Different strategies have been used to reduce the occurrence of plant diseases including pesticides, less susceptible cultivars, crop rotation, and other control measures, but their efficacy is usually insufficient due to the survival and resistance of soil-borne pathogens [3]. Moreover, the excessive use of synthetic pesticides has adverse effects on the environment and living organisms, and also disturbs ecosystem functioning and decreases agricultural sustainability [4].

Nowadays, research is directed to environmentally friendly alternatives for controlling plant pathogens and improving crop production, which are recommended within an integrated crop management system (ICMS) [5]. As an important component of an ICMS, biological control is defined as the use of beneficial organisms to reduce the negative effects of plant pathogens and promote

positive responses by the plant [6]. The most common approach to biological control is the selection of antagonistic microorganisms, studies on their mechanisms of action and development of a biocontrol preparation [7].

Bacillus species are among the most investigated biocontrol agents i.e., biopesticides which contribute to suppression of plant pathogens by antagonism and/or competition [8]. Inhibition of pathogen growth by *Bacillus* spp. entails the involvement of mechanisms such as competition for nutrients and space, production of antibiotics, hydrolytic enzymes, siderophores, and/or inducing systemic resistance [9]. *Bacillus* spp. also can act as biofertilizers or biostimulators, either by facilitating the uptake of certain nutrients from the environment (nitrogen fixation, phosphate solubilization), or by providing the plant with a compound (biosynthesis of plant hormones) [10].

Hence, *Bacillus* spp. represent an alternative to plant growth enhancement agrochemicals, i.e., synthetic pesticides and fertilizers. The beneficial effects of *Bacillus* spp. on plant growth and yield have been demonstrated in several agricultural crops including wheat, maize, soybean, sunflower, common bean, tomato, pepper, potato, cucumber, and many others [11]. Application of *Bacillus* spp. to increase the productivity of field and vegetable crops is limited by variability among the results obtained in the laboratory, greenhouse and field [12]. In fact, when reintroduced by plant/soil inoculation, only 1 to 2% of rhizobacteria exert a beneficial effect on plant growth [13]. Due to numerous factors that affect the effectiveness of *Bacillus* spp., it is necessary to understand how different strains deploy biocontrol and growth-promoting actions in plants, and clearly determine the traits and manner for selecting the best acting strains [12].

This review summarizes the different mechanisms utilized by *Bacillus* spp. in plant disease control and plant growth promotion, and focuses on the new approaches to the improvement of beneficial plant–*Bacillus* interactions and *Bacillus* spp. efficiency in the field.

2. Genus *Bacillus*

The genus *Bacillus* was established in 1872 by Cohn and encompasses over 200 described species and subspecies belonging to the *Firmicutes* phylum. Based on the morphological characteristics, bacteria of this genus are described as rod-shaped, Gram-positive, aerobic or facultatively anaerobic, and catalase-positive [14]. Due to their broad physiological ability and capability to form endospores, *Bacillus* spp. are resistant to adverse environmental conditions and omnipresent in a wide range of habitats, including soil. *Bacillus* spp. represent the predominant soil and rhizosphere bacteria, where they comprise up to 95% of the Gram-positive bacterial populations [15]. Furthermore, they are among the most widespread endophytic bacteria [16].

Bacillus is a large and diverse group of non-pathogenic and pathogenic bacteria. Most species of *Bacillus*, as well as their products, are considered safe for intended use in the environment [17]. These bacteria are preferred for commercialization for their ability to secrete several bioactive metabolites, produce extremely tolerant endospores, and grow rapidly in different media [18]. Consequently, they maintain viability and can be easily formulated and stored [19]. Populations of *Bacillus* spp. can successfully persist in the soil and plant rhizosphere without any perdurable effects on other bacterial populations [20]. Commercial *Bacillus*-based preparations are developed and distributed worldwide and contain beneficial strains of *Bacillus subtilis*, *Bacillus amyloliquefaciens*, *Bacillus pumilus*, *Bacillus licheniformis*, *Bacillus megaterium*, *Bacillus velezensis*, *Bacillus cereus*, *Bacillus thuringiensis*, etc., [21].

3. Mechanisms of Biological Control

3.1. Antibiotics

The antagonistic activities of *Bacillus* spp. are frequently related to the production of secondary metabolites with antibiotic properties. These compounds mainly involve peptides with low molecular weight that are generated ribosomally (bacteriocins) or non-ribosomally (lipopeptides, peptides, polyketides).

Bacteriocins are ribosomally synthesized peptides produced by numerous bacteria which might be useful against pathogenic and antibiotic-resistant bacteria [22]. Bacteriocins act against target cells by interfering with the synthesis of the cell wall or by forming pores in the cell membrane [23]. The antimicrobial mechanisms of bacteriocins are usually directed against the species which are the same or closely related to the producers, with a narrow spectrum of action. Nevertheless, due to the production of bacteriocins, *Bacillus* spp. exhibit a broad-spectrum of antibacterial activity [24]. Some reports identify bacteriocins and bacteriocin-like substances (BLSs) (amylolysin, amysin, subtilin, subtilosin A, subtilosin B, thuricin) isolated from various *Bacillus* spp., including *B. amyloliquefaciens, B. subtilis, B. thuringiensis, B. cereus,* and *B. coagulans* [25]. Isolation and characterization of bacteriocins and BLSs may have an important use in the biological control of the pathogenic bacteria. However, *Bacillus* spp., which produce non-ribosomally synthesized lipopeptides and peptides, exhibit much stronger antimicrobial activity [26].

Cyclic lipopeptides (LPs), well known for their antagonistic action against a wide range of plant pathogens, are the most thoroughly studied antibiotic compounds in *Bacillus* spp. [27]. These peptides are synthesized by large non-ribosomal peptide synthetases (NRPSs) [28]. The primary mechanisms of LPs' actions usually involve an interaction with the cell membrane of the target pathogens, causing changes in its structure and permeability through disruption, solubilization or formation of ion-conducting pores [26]. It has also been demonstrated that LPs interact with intracellular structures, such as DNA [29]. Recent investigations have shown that LPs influence colonization and persistence of *Bacillus* in the rhizosphere, and stimulate plant defense mechanisms [30].

The most important cyclic LPs from *Bacillus* spp. are represented by surfactin, iturin and fengycin families [27]. These antibiotics consist of amino acids, amino- or hydroxyl-fatty acids with different lengths of hydrocarbon chains. The surfactin family (surfactin, lichenysin, pumilacidin, halobacilin, bamilocyn) are heptapeptides, identified in *B. subtilis*, *B. amyloliquefaciens*, *B. licheniformis*, *B. pumilus* and *Bacillus coagulans*. Surfactins act as both antifungal and antibacterial agents. The iturin family (iturin, mycosubtilin, bacillomycin, bacillopeptins, mixirins, mojavensin, subtulene) consists of heptapeptides produced by *B. subtilis*, *B. amyloliquefaciens*, *Bacillus circulans*, *B. pumilus*, and *Bacillus vallismortis*. Iturins display inhibitory effects on a wide range of fungi, but are less active against bacteria. The fengycin family (fengycin, plipastatin, maltacin) are decapeptides of which production was detected in *B. subtilis* and *B. amyloliquefaciens*. Fengycins are useful in protecting plants against fungal pathogens [26–28].

Other non-ribosomally synthesized LPs include kurstakins, bacitracins, polymyxins, gramicidins, and tyrocidines. The kurstakins are cyclic or linear heptapeptides that are specific to the *B. cereus* and *B. thuringiensis*, with the ability to destabilize biological membranes of both bacteria and fungi [31]. Bacitracins are cyclic decapeptides produced by *B. licheniformis, B. subtilis*, and *B. sonorensis*, of which activity is primarily directed against Gram-positive bacteria [32]. Polymyxins are cyclic decapeptides produced by *Paenibacillus polymyxa* (*Bacillus polymyxa*), which inhibit Gram-negative bacterial cells. Gramicidins and tyrocidines are cyclic decapeptides produced by *Bacillus brevis*, active against a broad range of Gram-negative and Gram-positive bacteria [33].

Several *Bacillus* spp. are known to produce other non-ribosomally synthesized antibiotics, such as peptides (bacilysin, rhizocticin, amicoumacin, mycobacillin, diketopiperazines) and polyketides (bacillaene, dihydrobacillaene, difficidin, macrolactin), with diverse antifungal and antibacterial activities [34].

The most commonly used biocontrol agents, *B. subtilis* and *B. amyloliquefaciens*, dedicate 4–5% and 8.5% of total genetic capacity to synthesis of secondary metabolites, with the potential to produce more than two dozen structurally diverse antimicrobial compounds [27,35]. Nowadays, gene clusters encoding for bacteriocins, as well as peptides and polyketides, can be readily identified in genomic sequences by genome mining. In total, 583 putative bacteriocin gene clusters were identified from 328 strains of 57 Bacillales species, while 1231 putative non-ribosomal antimicrobial gene clusters were detected and sub-grouped into 23 types of peptide and five types of polyketide compounds distributed over 49 species of Bacillales [36].

Numerous studies revealed a broad antimicrobial effect by *Bacillus* spp. due to production of antibiotics (Table 1). *Bacillus* spp. mostly produce LPs from one family, while a few strains were identified as co-producers of different LPs [37]. Furthermore, antimicrobial activity of *Bacillus* spp. relies on the proportion and diversity in the production of antibiotics [38]. Fusarium clove rot of garlic, as well as head blight of wheat, were successfully suppressed by *B. subtilis* and/or *B. amyloliquefaciens*, due to LPs production [39,40]. In another study, *B. amyloliquefaciens* was defined as a producer of bacteriocins, surfactin, and fengycin, and was proven as a very potent biocontrol agent against numerous Gram-positive and Gram-negative bacteria, as well as *Fusarium oxysporum*, *Fusarium avenaceum*, and *Mucor* sp. [24]. Ongena et al. [41] found that iturin and fengycin produced by *B. subtilis*, which contributed to antifungal activity against *Pythium ultimum*. Han et al. [30] showed that iturin-producing *B. amyloliquefaciens* was effective in the biocontrol of *Verticillium dahliae*. Similarly, lipopeptides from *Bacillus* sp. and *B. amyloliquefaciens* such as surfactin, iturin, and fengycin, were responsible for antifungal activity against *Sclerotinia sclerotiorum* [42]. When tested for its biocontrol potential, *B. amyloliquefaciens* and *B. pumilus* LPs producing strains were very effective in the reduction in *Pseudomonas syringae* pv. *aptata* infection of sugar beet [43]. Additionally, Yang et al. [44] established that *B. subtilis* was able to suppress *Gaeumannomyces graminis* var. *tritici* infection of wheat through the production of LPs, namely iturin, surfactin, plipastatin, bacillomycin, and difficidin. Antifungal lipopeptide produced by *B. licheniformis*, determined as surfactin, was very successful against *Magnaporthe grisea*, a causative agent of rice blast [45]. Antifungal activity against *Rhizoctonia solani*, *Pythium aphanidermatum*, and *Sclerotium rolfsii* was attributed to *B. pumilus* because of the production of lipopeptide pumilacidin from the surfactin family [46].

Table 1. Biocontrol mechanisms exhibited by *Bacillus* species.

Bacillus Species	Mechanism (s)	Target Pathogen (s)	Plant Disease	Reference
Bacillus amyloliquefaciens	Bacteriocins, surfactin, fengycin	Various pathogenic bacteria, *Fusarium oxysporum*, *Fusarium avenaceum*, *Mucor* sp.	Several diseases of field and vegetable crops	[24]
Bacillus amyloliquefaciens	Iturin	*Verticillium dahliae*	Wilt of cotton	[30]
Bacillus amyloliquefaciens/Bacillus subtilis	Iturin, surfactin/surfactin, fengycin	*Fusarium graminearum*	Head blight of wheat	[39]
Bacillus subtilis	Surfactin, Lytic enzymes	*Fusarium* spp.	Clove rot of garlic	[40]
Bacillus subtilis	Iturin, fengycin	*Pythium ultimum*	Damping-off of bean	[41]
Bacillus sp., *Bacillus amyloliquefaciens*	Surfactin, iturin, fengycin, siderophore	*Sclerotinia sclerotiorum*	White mold of common bean	[42]
Bacillus pumilus, *Bacillus amyloliquefaciens*	Lipopeptides	*Pseudomonas syringae* pv. *aptata*	Leaf spot disease of sugar beet	[43]
Bacillus subtilis	Iturin, surfactin, plipastatin, bacillomycin, difficidin	*Gaeumannomyces graminis* var. *tritici*	Take-all of wheat	[44]
Bacillus licheniformis	Surfactin	*Magnaporthe grisea*	Blast disease of rice	[45]
Bacillus subtilis	Chitinase	*Rhizoctonia solani*	Stem canker and black scurf of potato	[47]
Bacillus amyloliquefaciens	Protease	*Fusarium oxysporum* f. sp. *lycopersici*	Wilt disease of tomato	[48]
Bacillus amyloliquefaciens	Siderophores, cellulase, lipase, protease, chitinase	*Clavibacter michiganensis*	Bacterial canker of tomato	[49]
Bacillus sp.	Protease, glucanase, chitinase, siderophores	*Fusarium verticillioides*	Stalk and ear rot of maize	[50]
Bacillus velezensis	Protease, Chitinase, Cellulase, Glucanase	*Botrytis cinerea*	Gray mold disease of pepper	[51]
Bacillus subtilis	Siderophores	*Fusarium oxysporum* f.sp. *capsici*	Wilt of pepper	[52]
Bacillus subtilis	Siderophores, lytic enzymes	*Bipolaris sorokiniana*	Spot blotch of wheat	[53]

3.2. Lytic Enzymes

Antimicrobial activity of *Bacillus* spp. could also be due to the production of hydrolytic enzymes such as chitinases, chitosanases, glucanases, cellulases, lipases, and proteases, which efficiently hydrolyze the major components of the fungal and bacterial cell walls.

Chitinases (EC 3.2.1.14) are glycoside hydrolases (GHs) which degrade the β-1,4-glycosidic bonds in chitin, the second most abundant naturally available polysaccharide after cellulose, and the main component of the fungal cell wall [54]. Bacteria primarily produce chitinases in order to degrade chitin for its utilization as an energy source, whereas some bacterial chitinases are prospective biological control agents against a variety of plant diseases caused by phytopathogenic fungi [47,55]. Chitosanases (E.C. 3.2.1.132) are GHs which catalyze the hydrolytic degradation of the β-1,4-glycosidic bonds in the chitin derivative-chitosan [56]. Chitosanases are important for the extensive carbon and nitrogen recycle [57]. Since chitosan is also found in fungal cell walls, chitosanase-producing *Bacillus* spp. may be used as biocontrol agents to prevent plant infection caused by pathogens [58]. Glucanases are GHs which hydrolyze glycosidic bonds present in α-glucans and β-glucans. α-1,3-glucan is not indispensable cell wall component, but plays an important role in some fungi during cell separation and vegetative growth [59], while β-1,3-glucan is the second major component of the fungal cell wall after chitin [60]. The primary role of cell wall glucans in fungi is structural, but they may also be degraded and used as nutritional sources. *Bacillus* spp. are a rich source of α-1,3-glucanase (EC 3.2.1.84) and β-1,3-glucanase (EC 3.2.1.39). The enzymes have previously been isolated from *Bacillus brevis*, *B. licheniformis*, *B. subtilis*, *B. circulans*, and *Bacillus halodurans* [61]. Besides chitin and glucan, the skeleton of fungal cell walls contains cellulose, lipids and proteins. Bacterial cellulases, lipases and proteases may, therefore, play a significant role in the cell wall lysis that occurs during pathogen–*Bacillus* interactions [48].

Successful cell wall degradation depends on the activity of more than one enzyme. Chitinase activity is preceded by, or coincides with, the hydrolytic activity of other enzymes, especially glucanases. Mixtures of hydrolytic enzymes with complementary modes of action may be required for maximum efficacy, while correct combinations of enzymes may increase antifungal activity [62].

Recently, several reports have documented the production of lytic enzymes from *Bacillus* spp. biocontrol agents (Table 1). Chitinase-producing *B. subtilis* was effective against *Rhizoctonia solani* [47]. Crude and purified protease of *B. amyloliquefaciens* showed efficacy in biocontrol of *Fusarium oxysporum* [48]. The potential of *B. amyloliquefaciens* for biocontrol of *Clavibacter michiganensis* ssp. *michiganensis* was attributed to the production of lytic enzymes (cellulase, lipase, protease, chitinase) [49]. Hydrolytic enzymes (protease, glucanase, chitinase) produced by *Bacillus* sp. were responsible for a strong inhibitory activity against *Fusarium verticillioides* causing stalk and ear rot of maize [50]. The strength of hydrolase activity (protease, chitinase, cellulase, glucanase) was the key factor of *B. velezensis* in control of pepper gray mold caused by *Botrytis cinerea* [51]. Generally, it has been found that strains of *Bacillus* spp. which have the ability to produce cell wall hydrolases are more effective in the suppression of plant pathogens [63]. In search of efficient biocontrol agents, isolation and characterization of enzyme-producing *Bacillus* spp. should be done in order to achieve maximum survival of bacteria under detrimental environmental conditions and intrusion of pathogens [40,64].

3.3. Siderophores

Siderophores are metal-chelating, non-ribosomal peptides with low molecular weight produced by some microorganisms and plants, especially under iron starvation conditions [65]. Iron (Fe) is an essential element for different biological processes such as oxygen metabolism, DNA and RNA syntheses, electron transfer, and enzymatic processes. The primary role of siderophores is to chelate Fe, allowing its solubilization and extraction from minerals and organic compounds. The significance of siderophores in biological control is based on competition for Fe in order to reduce its availability for pathogens [9]. Furthermore, microbial siderophores can be reduced to donate Fe to the transport system of a plant or chelate Fe from soils, and then, do a ligand exchange with phytosiderophores,

thus, providing plants with this essential element so as to enhance their growth [66]. In addition to Fe, siderophores also have the ability to bind a variety of metals in the environment, thereby acting as bioremediation agents [67].

Siderophores are grouped into three main families, depending on the functional group, including hydroxamates, catecholates, and carboxylates [9]. Most of the bacterial siderophores are catecholates, such as bacillibactin produced by several *Bacillus* spp. including *B. subtilis, B. amyloliquefaciens, B. cereus, B. thuringiensis,* etc., [68]. Besides bacillibactin, *Bacillus* spp. produce a wide variety of siderophores such as pyoverdine, pyochelin, schizokinen, petrobactin, etc., [69]. *Bacillus* spp. were better producers of siderophores than other bacterial isolates from the maize rhizosphere [70]. Siderophores produced by *Bacillus* spp. have been involved in suppression of several plant diseases (Table 1). For instance, siderophore-producing *B. subtilis* reduced the incidence of Fusarium wilt, and enhanced the growth and yield of pepper [52]. Several studies indicated synergistic antimicrobial effects of siderophores along with lipopeptides and/or lytic enzymes [42,49,50]. Similarly, *B. subtilis* is a promising biological control agent against *Bipolaris sorokiniana* due to production of siderophores, chitinase, and cellulase [53].

4. Systemically Induced Disease Resistance

Plants adapt to constant pathogen exposure through defense mechanisms. Resistance to pathogens, developed after proper stimulation, represents an improvement in the defense capacity of the plant. Infected plants increased their levels of signaling molecules which coordinate the activation genes for appropriate syntheses, followed by preventive structural and histological changes, preventative chemical substances (phenols and other products of secondary metabolism), and in other ways [71,72].

Plant defense mechanisms, such as induced systemic resistance (ISR), can be initiated by external agents before infection or triggered by a localized infection, resulting in systemic acquired resistance (SAR) [73]. Both biotic and abiotic factors have been used for inducing ISR in plants against different plant pathogens. ISR is promoted by non-pathogenic rhizobacteria, and is mostly dependent on the jasmonate (JA) and/or ethylene (ET) signaling pathways [74], while SAR is mediated via a salicylic acid (SA)-dependent process. SAR also activates specific sets of defense-related genes associated with the production of pathogenesis-related proteins (PR), while ISR is not accompanied by the activation of these genes [75]. The defense mediated by ISR is significantly weaker than that obtained by SAR. However, ISR and SAR together provide better protection, indicating that they can act additively in inducing resistance to pathogens [72].

Rhizobacteria promote ISR in plants through the production of various metabolites such as antibiotics, siderophores, volatile organic compounds (VOCs), and others [76]. *Bacillus* spp. are among the most studied rhizobacteria that trigger ISR in plants (Table 2), while being capable of inducing resistance against several pathogens in the same plant [77]. *B. amyloliquefaciens* induced salicylic acid-dependent resistance in tomato plants, reduced the incidence of *Tomato spotted wilt virus*, and delayed systemic accumulation of *Potato virus Y* [78]. Application of *B. cereus* significantly reduced disease incidence caused by *Botrytis cinerea* through activation of ISR [79]. Chandler et al. [80] showed that *B. subtilis* triggered ISR in rice against *Rhizoctonia solani* via jasmonic acid (JA) and ethylene (ET), as well as abscisic acid (ABA) and auxin signaling. The same authors reported an indispensable role of *B. subtilis* LPs, namely fengycin and surfactin, in the induced defense state. ISR promoting *B. amyloliquefaciens* produced VOCs and significantly reduced spot disease caused by *Xanthomonas axonopodis* pv. *vesicatoria* in pepper [81]. The ability of *B. megaterium* to reduce Septoria tritici blotch severity, caused by *Mycosphaerella graminicola*, was the result of a combination of different mechanisms, including ISR [82]. *Bacillus* endophytes of maize may protect host plants by producing antifungal lipopeptides that inhibit *Fusarium moniliforme* as well as by inducing the systemic acquired resistance [83].

Table 2. Induced systemic resistance elicited by *Bacillus* species.

Bacillus Species	Target Pathogen (s)	Plant Disease	Reference
Bacillus amyloliquefaciens	*Tomato spotted wilt virus, Potato virus Y*	Wilt disease of tomato	[78]
Bacillus cereus	*Botrytis cinerea*	Gray mold disease of field and vegetable crops	[79]
Bacillus subtilis	*Rhizoctonia solani*	Sheath blight of rice	[80]
Bacillus amyloliquefaciens	*Xanthomonas axonopodis* pv. *vesicatoria*	Leaf spot disease of pepper	[81]
Bacillus megaterium	*Mycosphaerella graminicola*	Septoria tritici blotch of wheat	[82]
Bacillus subtilis, Bacillus amyloliquefaciens	*Fusarium moniliforme*	Ear, stalk, and root rots of maize	[83]
Bacillus subtilis	*Alternaria solani, Phytophthora infestans*	Early and late blight of tomato	[84]
Bacillus spp.	*Pyricularia oryzae*	Blast disease of rice	[85]
Bacillus sp.	*Colletotrichum capsica*	Anthracnose of chili	[86]
Bacillus sp.	*Rhizoctonia solani, Fusarium oxysporum*	Root rot and wilt of soybean	[87]
Bacillus subtilis	*Fusarium oxysporum* f. sp. *cucumerinum*	Root rot of cucumber	[88]
Bacillus sp.	*Plasmopara halstedii*	Downy mildew of sunflower	[89]

Bacillus spp. can elicit ISR by inducing the synthesis of antioxidant defense enzymes. Host enzymes induced by *B. subtilis* include peroxidase (POX), polyphenol oxidase (PPO), phenylalanine ammonia-lyase (PAL), and superoxide dismutase (SOD). Increased synthesis of antioxidant defense enzymes results in ISR against early and late blight in tomato seedlings [84]. Similarly, Rais et al. [85] showed that *Bacillus* spp. enhanced the SOD, POX, PPO, and PAL activities in infected rice, thus, alleviating *Pyricularia oryzae*-induced oxidative damage and suppressing blast disease incidence. The antagonistic *Bacillus* sp. suppressed anthracnose disease of chili by the activation of defense-related enzymes and the accumulation of phenolic compounds [86]. Similarly, *Bacillus* sp. enhanced growth promotion and protection against *Rhizoctonia solani* and *Fusarium oxysporum* by the eliciting of defense-related enzymes (PAL, POX, PPO) in soybean [87], while *B. subtilis* was capable of impairing disease incidence, promoting seedling growth and increasing activities of antioxidant enzymes (POD, PPO, PAL) in cucumber plants [88]. The induction of resistance to *Plasmopara halstedii* by *Bacillus* sp. strain was accompanied by the accumulation of defense-related enzymes (PAL, POX, PPO) in sunflower [89].

5. Mechanisms of Plant Growth Promotion

5.1. Nutrient Availability

Bacillus spp. produce numerous metabolites which can increase nutrient availability to plants, and thus, directly promote plant growth and yield. Most of the plant essential nutrients are supplied through mineral fertilization, a practice which causes major economic losses, as well as posing significant problems to the environment. The use of biofertilizers which contain N_2-fixing and/or P-solubilizing *Bacillus* spp. is a reasonable approach to reducing the negative impacts of synthetic fertilizers without compromising food safety [5,17]. N_2-fixing and P-solubilizing *Bacillus* spp. are directly related to nutrient uptake and the subsequent growth promotion in different plants (Table 3).

Nitrogen (N) is essential for plant growth, albeit largely unavailable in its atmospheric form (more than 80%) [90]. Biological nitrogen fixation (BNF) is carried out by several groups of microorganisms that are able to absorb elemental nitrogen from the atmosphere and form compounds, which serve as plant nutrients [91]. The microorganisms produce the enzyme nitrogenase in order to catalyze the

conversion of molecular dinitrogen (N_2) to ammonia (NH_3), which is subsequently taken by plant roots and assimilated in amino acids. BNF provides Earth's ecosystems with about 200 million tons N per year [92]. The nitrogen-fixing microorganisms are either free-living or symbiotic. Several PGPR, including *Bacillus* spp. can decrease chemical fertilizer-N use and increase plant growth and yield through asymbiotic nitrogen fixation. BNF by rhizobacteria has been reported to contribute up to 12–70% of total N uptake in agricultural crops. The study of Kuan et al. [93] provided evidence that *B. pumilus* can fix atmospheric N_2 and significantly increase the total N content and dry biomass of maize. Ding et al. [94] suggested that the *nifH* gene could be detected in both the *Bacillus* and *Paenibacillus* genera. Similarly, the study of Xie [95] reported nitrogenase activities of several *Bacillus* spp. including *B. megaterium*, *B. cereus*, *B. pumilus*, *B. circulans*, *B. licheniformis*, *B. subtilis*, *B. brevis*, and *B. firmus*. Szilagyi-Zecchin et al. [96] reported that endophytic *Bacillus* spp. were positive for the nitrogen fixation ability evaluated through the acetylene reduction assay and amplification of *nifH* gene. Increased relative abundance of *Bacillus* spp. in rice plants under the conditions of low nitrogen suggest the potential contribution of their BNF [97].

Table 3. Plant growth-promoting mechanisms exhibited by *Bacillus* species.

Bacillus Species	Mechanism (s)	Treated Plant (s)	Effect	Reference
Bacillus pumilus	N_2-fixation	Maize	Increase the total N content and dry biomass	[93]
Bacillus sp.	N_2-fixation	Maize	Increased seed germination and root volume	[96]
B. megaterium, *B. subtilis*, *B. simplex*	P-solubilization	Eggplant, pepper, tomato	Promoted seed germination and vegetative growth	[98]
Bacillus subtilis	P-solubilization	Cucumber	Increased plant growth, total accumulation of P and P uptake	[99]
Bacillus subtilis	IAA, GA	Tomato	Enhanced shoot and root growth, seedling vigor and leaf area, higher levels of hormones	[84]
Bacillus methylotrophicus	GAs	Lettuce	Increased shoot length, shoot fresh weight, leaf width, proteins, amino acids, macro and micro minerals, carotenoids and chlorophyll a	[100]
Bacillus subtilis	CKs	Lettuce	Increased plant shoot and root weight, higher CKs levels	[101]
Bacillus megaterium	CKs	Common bean	Promoted growth of seedlings	[102]
Bacillus spp.	IAA, CKs, GAs, ABA	Soybean	Better growth and higher proline contents	[103]
Bacillus subtilis	IAA, ACC deaminase	Tomato	Increased shoot and root biomass and chlorophyll (a and b) contents	[104]
Bacillus aryabhattai	ABA, IAA, CKs, GAs	Soybean	Longer roots and shoots, higher hormone levels, better stress tolerance	[105]
Bacillus amyloliquefaciens	ABA	Rice	Increased growth and stress tolerance	[106]

In addition to nitrogen, the plant growth directly depends on phosphorus (P). However, a high amount of P (more than 80%) is fixed in soil and is unavailable for plant uptake due to adsorption, precipitation or conversion [107]. Microorganisms that dissolve organic and inorganic phosphates belong to the group designated as Phosphate Solubilization Microorganisms (PSM) [108]. These microorganisms solubilize insoluble inorganic P and mineralize insoluble organic P [109]. Mechanisms

of inorganic phosphate solubilization by microorganisms involve the production of organic and inorganic acids, siderophores, protons, hydroxyl ions, and CO_2, which chelate cations or reduce pH in order to release P [110]. Mineralization of organic phosphate occurs due to the synthesis of extracellular enzymes such as phosphatases, phytases, and phospholipases [111].

Plant/soil inoculation with PSM is a promising strategy for the enhancement of plant absorption of P, while *Bacillus* spp. are among the most powerful PSM. Saeid et al. [112] showed that solubilizing exudates produced by *Bacillus* (*B. subtilis, B. megaterium, B. cereus*) are composed of gluconic, lactic, acetic, and succinic acids, confirming strong correlation between the total concentrations of organic acids and the amounts of released phosphorus. Isolates of *B. megaterium*, *B. subtilis*, and *B. simplex*, exhibited P-solubilizing ability by producing acetic, propionic, isobutyric, isocaproic, caproic, and heptanoic acids, and had positive effects on the seed germination and vegetative growth parameters of eggplant, pepper, and tomato [98]. Tao et al. [113] suggested that P-solubilization and P-mineralization could coexist in the same *Bacillus* strain. Similarly, inoculation with *B. subtilis* increased plant growth, and total accumulation of P and P uptake by cucumber plants [99].

5.2. Phytohormone Production

Bacillus spp. may directly increase plant yield through mechanisms that impart the production of phytohormones or plant growth regulators (PGRs), such as auxins, cytokinins, gibberellins, ethylene, and abscisic acid. Plant hormones are organic substances that influence the physiology and development of plants at very low concentrations. Plant hormone biosynthesis by *Bacillus* spp. has been directly related to subsequent growth promotion in different plants (Table 3).

Auxins are a group of plant hormones that stimulate plant growth, mainly through the regulation of cell division, cell elongation, and tissue differentiation. The main naturally occurring auxin is indole-3-acetic acid (IAA) [114]. Different bacteria, including *Bacillus* spp., have the ability to produce IAA and use this phytohormone to interact with plants as part of their colonization strategy, including phytostimulation and circumvention of basal plant defense mechanisms [80]. Production of IAA is widespread among soil bacteria, and approximately 80% of rhizobacteria have been estimated to produce IAA [115]. The *in vitro* application of IAA-producing *Bacillus* strains on plant roots resulted in increases in root length as well as the number of lateral roots [116]. *B. subtilis* was reported to enhance shoot and root growth, seedling vigor and leaf area of tomato, while higher levels of gibberellins and IAA were detected in treated plants [84]. Recent studies demonstrated that *Bacillus* spp. play a major role in controlling endogenous IAA levels in plant roots by regulating the auxin-responsive genes, thereby causing changes in root architecture [117].

Gibberellins (GAs) are a group of plant hormones that affect many developmental processes in higher plants, including seed germination, stem elongation, flowering, and fruiting. Gutierrez-Manero et al. [118] documented the production of gibberellins by *B. pumilus* and *B. licheniformis*. The beneficial effect of *Bacillus methylotrophicus* on plants due to the secretion of an array of gibberellins was confirmed by increasing the percentage of seed germination of lettuce, muskmelon, soybean, and vegetable mustard [100]. The same authors established that GA-producing bacterial strain increased shoot length, shoot fresh weight, leaf width, proteins, amino acids, macro and micro minerals, carotenoids and chlorophyll in lettuce.

Cytokinins (CKs) are a group of plant hormones that play a key role in promoting cell division, or cytokinesis, in plant roots and shoots. They are important regulators of other physiological and developmental plant processes such as seed germination, apical dominance, nutrient mobilization, and leaf senescence. Plants and microorganisms produce about 30 compounds from the group of CKs. It has been found that 90% of phosphate-dissolving rhizobacteria have the ability to produce CKs in vitro [119]. Arkhipova et al. [101] reported the ability of *B. subtilis* to produce CKs, while inoculation of lettuce plants increased the cytokinin content of both shoots and roots, as well as plant shoot and root weight. Ortíz-Castro et al. [102] reported that *B. megaterium* promoted the growth of *Arabidopsis*

thaliana and *Phaseolus vulgaris* seedlings through CKs production. Naz et al. [103] also perceived that cytokinin-producing species, such as *Bacillus* and others, stimulated the growth of soybean plants.

Ethylene is a gaseous plant hormone that mainly regulates maturation and senescence processes, as well as response to biotic and abiotic stresses. In addition to plants, ethylene production was established in bacteria and fungi, but little has been reported on how ethylene-producing microorganisms affect plant growth. Several PGPR, including *Bacillus* spp., synthesize the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase that modulates ethylene levels in plants which might otherwise become growth inhibitory [120]. The enzyme ACC deaminase (3.5.99.7) cleaves ACC (direct precursor of ethylene biosynthesis in plants) into ammonia and α-ketobutyrate. Bacteria characterized by ACC deaminase activity can help maintain plant growth and development under stress conditions (drought, salt, flooding and anoxia, the presence of pathogens or contaminants) [121]. The interaction of plants with ACC deaminase-producing bacteria may be expected to promote plant growth during plant processes associated with local increase in ethylene concentration, like flower wilting or symbiosis establishment [122]. Although ACC deaminase activity has been described in many *Bacillus* strains [104,123], ACC deaminase genes (structural gene *acdS* and the regulatory gene *acdR*) could not be identified in 271 completely sequenced strains belonging to the Bacilli class, including many soil and plant-associated *Bacillus* and *Paenibacillus* species [124].

Abscisic acid (ABA) is a plant hormone with an important role in many plant physiological processes, including seed germination and stress tolerance. Park et al. [105] showed that *Bacillus aryabhattai* produced significant amounts of ABA, IAA, CKs, and GAs in culture, while inoculated soybean plants had high levels of phytohormones, longer roots and shoots, and better tolerance to heat, oxidative, and nitrosative stress. The bacterial endophyte *B. amyloliquefaciens* has been found to produce ABA and increase plant growth and resistance to salinity stress [106].

6. Efficient Use and New Approaches

6.1. Isolation and Identification

Prior to characterization and selection in laboratory and in greenhouse/field conditions, the search for effective strains requires isolation and identification of preferred *Bacillus* species from different sources. *Bacillus* spp. are the predominant soil, rhizosphere and endophytic bacteria [15,16]. Considering a very small proportion of beneficial microorganisms in the rhizosphere, their isolation, multiplication, and inoculation into the plant/soil trigger microbiological processes and intensify overall microbial activity [70]. Thus, only a few *Bacillus* spp. of about 200 within the genus exhibit multiple plant growth-promoting traits and might be useful in formulating inoculants [21]. Identification of isolated *Bacillus* spp. is of great importance because their beneficial traits are characteristic of certain species. Accordingly, it is necessary to use methods that can quickly and reliably test a large number of *Bacillus* spp. as the potential plant growth promoters and biological control agents.

Determination of morphological, physiological and biochemical traits is a long and often unreliable process. The most accurate method for examining the diversity of *Bacillus* spp. is their identification and characterization at the molecular level. The NCBI (National Center for Biotechnology Information) and RDP (Ribosomal Database Project) databases contain 2611 individual 16S rDNA sequences originating from 175 different species of *Bacillus*, of which only 1586 have been identified to the species level [125]. In addition to standard molecular methods such as 16S rRNA analysis, RFLP (Restriction Fragment Length Polymorphism), RAPD (Random Amplified Polymorphic DNA), rep-PCR (Repetitive element sequence-based Polymerase Chain Reaction), MLSA (Multilocus Sequence Analysis), etc., different PCR methods with species-specific primers are increasingly used for reliable differentiation of *Bacillus* spp. [126].

6.2. Characterization and Selection

The characterization of bacteria includes determination of numerous traits in laboratory, while selection of potential biofertilizers and biopesticides involves testing their effectiveness on the plant–soil system in greenhouse and/or field. The tests require a lot of time, which makes it impossible to examine a large number of strains. Given that no individual or combined traits can reliably predict the effectiveness in biocontrol and plant growth promotion, Akinrinlola et al. [90] suggested greenhouse pot tests as the first criterion for bacterial strain selection, instead of screening bacteria for multiple traits. According to reports, the effectiveness of *Bacillus* spp. frequently varies depending on specific plant and soil conditions, which can constrain their ability to colonize the rhizosphere and express beneficial traits [12].

The efficiency of inoculation is usually higher when bacteria are isolated from the rhizosphere of plant species, and/or soil that will be inoculated, suggesting that the growth-promoting ability of the strains is highly related to certain plant species and soil types [12]. Furthermore, the efficiency of *Bacillus* spp. from the rhizosphere is higher compared to those from the bulk soil, while both the rhizosphere and endophytic bacteria possess various beneficial traits regarding the number and the production amount of these characteristics [127]. Knowledge of biocontrol and plant growth promotion mechanisms of *Bacillus* spp. is very important for their intended use, for instance, the use of LPs and hydrolase-producing strains in the suppression of pathogen infection, or P-solubilizing and N_2-fixing strains in P and N-deficient soils. Their efficiency as individual and combined plant/soil inoculants in different environments needs to be established through continuous selection of effective isolates in greenhouse and field trials.

6.3. Plant–Bacillus Interactions

Successful application of *Bacillus* spp. in the field also depends on plant–*Bacillus* interactions and it can be limited by poor colonization of the rhizosphere [128]. *Bacillus* spp. require 24 h to form a biofilm, which contributes to root colonization of *Bacillus* spp. and extends their beneficial effects in the soil [129]. Transcriptomic analysis of the *B. amyloliquefaciens* genome revealed numerous genes included in rhizosphere habituation and plant-beneficial traits, such as plant polysaccharide utilization, cell motility and chemotaxis, secondary antibiotics synthesis, and plant growth promotion-relevant clusters [130]. Gao et al. [128] demonstrated that both chemotaxis and swarming motility are important in tomato root colonization by *B. subtilis*, while the part of swarming is greater than that of chemotaxis.

However, root colonization is more effectual in indigenous strains of *Bacillus* than in laboratory or commercial strains. Emerging strategies such as microbiome engineering and breeding of microbe-optimized crops can directly or indirectly detect, modulate and enhance the traits and ways for better performance of *Bacillus* strains [3,18]. The genes involved in root colonization and plant–*Bacillus* interactions, are induced by the presence of root and seed exudates [129–131]. New research in plant–bacteria interactions uncovers plant capability to shape their rhizosphere and endorhiza microbiome [127]. Recent studies of the rhizobiome and the utilization of next-generation sequencing (NGS) techniques, combined with proteomics, metagenomics, metabolomics, etc., will assist to elaborate on these interactions, including how this relationship affects plant health and growth [132].

6.4. Bacillus-Based Preparations

In recent years, the distribution of commercial *Bacillus*-based preparations has significantly increased worldwide (Table 4). In addition to their beneficial influence on plants, effective strains of *Bacillus* spp. should be able to persist in the environment and be stable and viable for extended storage and purposeful use in the field. Resistance and stability are among the major limitations of *Bacillus*-based preparations. These bacteria are suitable for commercialization due to their ability to secrete various metabolites, produce endospores, and grow rapidly in different media [17–20].

Endospores of *Bacillus* spp. can not only endure adverse environmental conditions but survive all processing phases during production. In order to enhance sporulation and synthesis of preferable metabolites, production of *Bacillus*-based preparations should be optimized at each stage, which implies selection of appropriate strains or consortium of strains, as well as cultivation and formulation process [133].

Table 4. Examples of commercial *Bacillus*-based preparations.

Bacillus Species	Preparation	Plant (s)	Company
Bacillus subtilis	Serenade®	Vegetables, fruits	AgraQuest Inc., USA
Bacillus subtilis	Companion®	Legumes, vegetables, maize, and others	Growth Products Ltd., USA
Bacillus subtilis	Kodiak®	Legumes, cotton, and others	Gustafson Inc., USA
Bacillus subtilis	Cease®	Several crops	BioWorks Inc., USA
Bacillus subtilis	Subtilex®	Vegetables, legumes, cotton, and others	Becker Underwood, Inc., USA
Bacillus subtilis	Pro-Mix®	Soybean, ornamentals, and others	Premier Horticulture Inc., Canada
Bacillus subtilis	FZB24®	Several crops	ABiTEP GmbH, Germany
Bacillus subtilis	Bio Safe®	Legumes, vegetables, cotton	Lab. Biocontrole Farroupilha, Brazil
Bacillus subtilis	Ecoshot®	Vegetables, legumes, fruits, and others	Kumiai Chemical Industry, Japan
Bacillus subtilis	Biosubtilin®	Cereals, vegetables, legumes, oilseeds, cotton, and others	Biotech International Ltd., India
Bacillus amyloliquefaciens	BioYield®	Legumes, vegetables, tobacco	Gustafson Inc., USA
Bacillus amyloliquefaciens	Rhizocell GC®	Cereals, sugar beet	Lallemand Plant Care, France
Bacillus amyloliquefaciens	RhizoVital®42, RhizoVital®42TB	Vegetables, cereals, ornamentals	ABiTEP GmbH, Germany
Bacillus pumilus	Ballad® Plus	Cereals, oilseeds, sugar beet, sweet corn	AgraQuest Inc., USA
Bacillus pumilus	Yield Shield®	Legumes, cereals, vegetables, sugar beet, cotton	Bayer CropScience, USA
Bacillus pumilus	Sonata®	Vegetables, fruits	AgraQuest Inc., USA
Bacilluslicheniformis	EcoGuard®	Several crops	Novozymes A/S Denmark, Novozymes Biologicals, USA
Bacillus velezensis	Botrybel®	Vegetables, fruits	Agricaldes, Spain
Bacillus megaterium	Symbion-P®	Cereals, legumes, oilseeds, vegetables	T. Stanes & Co. Ltd., India
Bacillus sp.	Sublic®	Several crops	ELEP Biotechnologies, Italy
Bacillus spp.	*Bacillus* SPP®	Several crops	Bio Insumos Nativa, Chile

Selection of appropriate *Bacillus* strains must be performed so as to avoid competition, especially if a preparation contains more than one species. For instance, interspecies competition between biofilms of the soil-residing bacteria *B. subtilis* and related *Bacillus* species could negatively affect their formulation and efficient use [134]. Nutrient sources such as carbon, nitrogen, inorganic salts and additional substances, as well as environmental factors such as temperature, pH value and O_2 supply, influence growth in addition to the production of spores and metabolites in *Bacillus* species [135]. *Bacillus* spp. are suitable for preparation as either solid or liquid formulations, with the addition of different carriers, stabilizers, protectants and other supplements [133]. Further research should find

the best possible production technology for each bacterial strain or bacterial combination, while taking into account the cost-effectiveness of *Bacillus*-based products.

7. Conclusions

Bacillus spp. represent an environmentally friendly strategy for crop production improvement through different mechanisms of biological control, biofertilization and biostimulation. Although possibilities to use *Bacillus* spp. for disease incidence reduction and crop production improvement are well known, their application is not a widespread practice, mostly because of inconsistent efficiency under different conditions. The ability of *Bacillus* spp. to exhibit beneficial traits depends on the interaction of bacteria with plant and/or pathogen, and the environment. Given the great economic and ecological importance of *Bacillus* spp., it is necessary to increase the number of practically important species and find advanced methods for their rapid and comprehensive research and efficient application.

References

1. Chakraborty, S.; Newton, A.C. Climate change, plant diseases and food security: An overview. *Plant Pathol.* **2011**, *60*, 2–14. [CrossRef]
2. Savary, S.; Ficke, A.; Aubertot, J.; Hollier, C. Crop losses due to diseases and their implications for global food production losses and food security. *Food Secur.* **2012**, *4*, 519–537. [CrossRef]
3. Syed Ab Rahman, S.F.; Singh, E.; Pieterse, C.M.J.; Schenk, P.M. Emerging microbial biocontrol strategies for plant pathogens. *Plant Sci.* **2018**, *267*, 102–111. [CrossRef]
4. Aktar, W.; Sengupta, D.; Chowdhury, A. Impact of pesticides use in agriculture: Their benefits and hazards. *Interdiscip. Toxicol.* **2009**, *2*, 1–12. [CrossRef]
5. Souza, R.; Ambrosini, A.; Passaglia, L.M.P. Plant growth-promoting bacteria as inoculants in agricultural soils. *Genet. Mol. Biol.* **2015**, *38*, 401–419. [CrossRef] [PubMed]
6. Lazarovits, G.; Turnbull, A.; Johnston-Monje, D. Plant Health Management: Biological Control of Plant Pathogens. In *Encyclopedia of Agriculture and Food Systems*; Van Alfen, N.K., Ed.; Academic Press: London, UK, 2014; Volume 4, pp. 388–399.
7. Alabouvette, C.; Olivain, C.; Steinberg, C. Biological control of plant diseases: The European situation. *Eur. J. Plant Pathol.* **2006**, *114*, 329–341. [CrossRef]
8. Mnif, I.; Ghribi, D. Potential of bacterial derived biopesticides in pest management. *Crop Prot.* **2015**, *77*, 52–64. [CrossRef]
9. Beneduzi, A.; Ambrosini, A.; Passaglia, L.M.P. Plant growth-promoting rhizobacteria (PGPR): Their potential as antagonists and biocontrol agents. *Genet. Mol. Biol.* **2012**, *4*, 1044–1051. [CrossRef]
10. Borriss, R. Use of Plant-Associated *Bacillus* Strains as Biofertilizers and Biocontrol Agents in Agriculture. In *Bacteria in Agrobiology: Plant Growth Responses*; Maheshwari, D.K., Ed.; Springer: Berlin/Heidelberg, Germany, 2011; pp. 41–76.
11. Aloo, B.N.; Makumba, B.A.; Mbega, E.R. The potential of Bacilli rhizobacteria for sustainable crop production and environmental sustainability. *Microbiol. Res.* **2019**, *219*, 26–39. [CrossRef]
12. Mrkovački, N.; Bjelić, D. Plant growth promoting rhizobacteria (PGPR) and their effect on maize. *Ratar. I Povrt.* **2011**, *48*, 305–312. [CrossRef]
13. Antoun, H.; Kloepper, J.W. Plant Growth Promoting Rhizobacteria. In *Encyclopedia of Genetics*; Brenner, S., Miller, J.H., Eds.; Academic Press: New York, NY, USA, 2001; pp. 1477–1480.
14. Logan, N.A.; De Vos, P. Genus *Bacillus*. In *Bergey's Manual of Systematic Bacteriology*, 2nd ed.; De Vos, P., Garrity, G.M., Jones, D., Krieg, N.R., Ludwig, W., Rainey, F.A., Schleifer, K.H., Whitman, W.B., Eds.; Springer: Dordrecht, The Netherlands; Berlin/Heidelberg, Germany; London, UK; New York, NY, USA, 2009; Volume 3, pp. 21–128.

15. Prashar, P.; Kapoor, N.; Sachdeva, S. Rhizosphere: Its structure, bacterial diversity and significance. *Rev. Environ. Sci. Biotechnol.* **2013**, *13*, 63–77. [CrossRef]

16. De Silva, N.I.; Brooks, S.; Lumyong, S.; Hyde, K.D. Use of endophytes as biocontrol agents. *Fungal Biol. Rev.* **2019**, *33*, 133148. [CrossRef]

17. Bhattacharyya, P.N.; Goswami, M.P.; Bhattacharyya, L.H. Perspective of beneficial microbes in agriculture under changing climatic scenario: A review. *J. Phytol.* **2016**, *8*, 26–41. [CrossRef]

18. Wu, L.; Wu, H.-J.; Qiao, J.; Gao, X.; Borriss, R. Novel routes for improving biocontrol activity of *Bacillus* based bioinoculants. *Front. Microbiol.* **2015**, *6*, 1395. [CrossRef] [PubMed]

19. Czaja, K.; Góralczyk, K.; Struciński, P.; Hernik, A.; Korcz, W.; Minorczyk, M.; Łyczewska, M.; Ludwicki, J.K. Biopesticides–towards increased consumer safety in the European Union. *Pest Manag. Sci.* **2015**, *71*, 3–6.

20. Radhakrishnan, R.; Hashem, A.; Abd Allah, E.F. *Bacillus*: A biological tool for crop improvement through bio-molecular changes in adverse environments. *Front. Physiol.* **2017**, *8*, 667. [CrossRef]

21. Mazzola, M.; Freilich, S. Prospects for biological soilborne disease control: Application of indigenous versus synthetic microbiomes. *Phytopathology* **2017**, *107*, 256–263.

22. Zou, J.; Jiang, H.; Cheng, H.; Fang, J.; Huang, G. Strategies for screening, purification and characterization of bacteriocins. *Int. J. Biol. Macromol.* **2018**, *117*, 781–789. [CrossRef]

23. Juturu, V.; Wu, J.C. Microbial production of bacteriocins: Latest research development and applications. *Biotechnol. Adv.* **2018**, *36*, 2187–2200. [CrossRef]

24. Salazar, F.; Ortiz, A.; Sansinenea, E. Characterisation of two novel bacteriocin-like substances produced by *Bacillus amyloliquefaciens* ELI149 with broad-spectrum antimicrobial activity. *J. Glob. Antimicrob. Resist.* **2017**, *11*, 177–182. [CrossRef]

25. Abriouel, H.; Franz, C.M.A.P.; Omar, N.B.; Gálvez, A. Diversity and applications of *Bacillus* bacteriocins. *FEMS Microbiol. Rev.* **2011**, *35*, 201–232. [CrossRef] [PubMed]

26. Fira, D.J.; Dimkić, I.; Berić, T.; Lozo, J.; Stanković, S. Biological control of plant pathogens by *Bacillus* species. *J. Biotechnol.* **2018**, *285*, 44–55. [CrossRef] [PubMed]

27. Stein, T. *Bacillus subtilis* antibiotics: Structures, synthesis and specific functions. *Mol. Microbiol.* **2005**, *56*, 845–857. [CrossRef] [PubMed]

28. Cawoy, H.; Debois, D.; Franzil, L.; De Pauw, E.; Thonart, P.; Ongena, M. Lipopeptides as main ingredients for inhibition of fungal phytopathogens by *Bacillus subtilis/amyloliquefaciens*. *Microb. Biotechnol.* **2015**, *8*, 281–295. [CrossRef] [PubMed]

29. Zhang, B.; Dong, C.; Shang, Q.; Han, Y.; Li, P. New insights into membrane-active action in plasma membrane offungal hyphae by the lipopeptide antibiotic bacillomycin L. *Biochim. Biophys. Acta Biomembr.* **2013**, *1828*, 2230–2237. [CrossRef]

30. Han, Q.; Wu, F.; Wang, X.; Qi, H.; Shi, L.; Ren, A.; Liu, Q.; Zhao, M.; Tang, C. The bacterial lipopeptide iturins induce *Verticillium dahliae* cell death by affecting fungal signaling pathways and mediate plant defence responses involved in pathogen-associated molecular pattern-triggered immunity. *Environ. Microb.* **2015**, *17*, 1166–1188. [CrossRef]

31. Gélis-Jeanvoine, S.; Canette, A.; Gohar, M.; Caradec, T.; Lemy, C.; Gominet, M.; Jacques, P.; Lereclus, D.; Slamti, L. Genetic and functional analyses of krs, a locus encoding kurstakin, a lipopeptide produced by *Bacillus thuringiensis*. *Res. Microbiol.* **2017**, *168*, 356–368. [CrossRef] [PubMed]

32. Adimpong, D.B.; Sørensen, K.I.; Thorsen, L.; Stuer-Lauridsen, B.; Abdelgadir, W.S.; Nielsen, D.S.; Derkx, P.M.F.; Jespersen, L. Antimicrobial susceptibility of *Bacillus* strains isolated from primary starters for African traditional bread production and characterization of the bacitracin operon and bacitracin biosynthesis. *Appl. Environ. Microbiol.* **2012**, *78*, 7903–7914. [CrossRef] [PubMed]

33. Wan, Y.; Stanovych, A.; Gori, D.; Zirah, S.; Kouklovsky, C.; Alezra, V. β, γ-diamino acids as building blocks for new analogues of Gramicidin S: Synthesis and biological activity. *Eur. J. Med. Chem.* **2018**, *149*, 122–128. [CrossRef] [PubMed]

34. Wang, T.; Liang, Y.; Wu, M.; Chen, Z.; Lin, J.; Yang, L. Natural products from *Bacillus subtilis* with antimicrobial properties. *Chin. J. Chem. Eng.* **2015**, *23*, 744–754. [CrossRef]

35. Chen, X.H.; Koumoutsi, A.; Scholz, R.; Schneider, K.; Vater, J.; Süssmuth, R.; Piel, J.; Borriss, R. Genome analysis of *Bacillus amyloliquefaciens* FZB42 reveals its potential for biocontrol of plant pathogens. *J. Biotechnol.* **2009**, *140*, 27–37. [CrossRef]

36. Zhao, X.; Kuipers, O.P. Identification and classification of known and putative antimicrobial compounds produced by a wide variety of Bacillales species. *BMC Genom.* **2016**, *17*, 882. [CrossRef]

37. Ongena, M.; Jacques, P. *Bacillus* lipopeptides: Versatile weapons for plant disease biocontrol. *Trends Microbiol.* **2008**, *16*, 115–125. [CrossRef]

38. Meena, K.R.; Kanwar, S.S. Lipopeptides as the antifungal and antibacterial agents: Applications in food safety and therapeutics. *Biomed Res. Int.* **2015**, *2015*, 473050. [CrossRef] [PubMed]

39. Zalila-Kolsi, I.; Mahmoud, A.B.; Ali, H.; Sellami, S.; Nasfi, Z.; Tounsi, S.; Jamoussi, K. Antagonist effects of *Bacillus* spp. strains against *Fusarium graminearum* for protection of durum wheat (*Triticum turgidum* L. subsp. *durum). Microbiol. Res.* **2016**, *192*, 148–158. [CrossRef] [PubMed]

40. Bjelić, D.; Ignjatov, M.; Marinković, J.; Milošević, D.; Nikolić, Z.; Gvozdanović-Varga, J.; Karaman, M. *Bacillus* isolates as potential biocontrol agents of *Fusarium* clove rot of garlic. *Zemdirbyste* **2018**, *105*, 369–376. [CrossRef]

41. Ongena, M.; Jacques, P.; Touré, Y.; Destain, J.; Jabrane, A.; Thonart, P. Involvement of fengycin-type lipopeptides in the multifaceted biocontrol potential of *Bacillus subtilis*. *Appl. Microbiol. Biotechnol.* **2005**, *69*, 29–38. [CrossRef]

42. Sabaté, D.C.; Pérez Brandan, C.; Petroselli, G.; Erra-Balsells, R.; Audisio, M.C. Biocontrol of *Sclerotinia sclerotiorum* (Lib.) de Bary on common bean by native lipopeptide-producer *Bacillus* strains. *Microbiol. Res.* **2018**, *211*, 21–30. [CrossRef]

43. Nikolić, I.; Berić, T.; Dimkić, I.; Popović, T.; Lozo, J.; Fira, D.; Stanković, S. Biological control of Pseudomonas syringae pv. aptata on sugar beet with *Bacillus pumilus* SS-10.7 and *Bacillus amyloliquefaciens* (SS-12.6 and SS-38.4) strains. *J. Appl. Microbiol.* **2019**, *126*, 165–176. [CrossRef] [PubMed]

44. Yang, L.; Han, X.; Zhang, F.; Goodwin, P.H.; Yang, Y.; Li, J.; Xia, M.; Sun, R.; Jia, B.; Zhang, J.; et al. Screening *Bacillus* species as biological control agents of *Gaeumannomyces graminis* var. *tritici on wheat. Biol. Control* **2018**, *118*, 1–9. [CrossRef]

45. Tendulkar, S.R.; Saikumari, Y.K.; Patel, V.; Raghotama, S.; Munshi, T.K.; Balaram, P.; Chattoo, B.B. Isolation, purification and characterization of an antifungal molecule produced by *Bacillus licheniformis* BC98, and its effect on phytopathogen *Magnaporthe grisea*. *J. Appl. Microbiol.* **2007**, *103*, 2331–2339. [CrossRef]

46. De Melo, F.M.P.D.; Fiore, M.F.; Moraes, L.A.B.D.; Silva-Stenico, M.E.; Scramin, S.; Teixeira, M.D.A.; Melo, I.S.D. Antifungal compound produced by the cassava endophyte *Bacillus pumilus* MAIIIM4A. *Sci. Agric.* **2009**, *66*, 583–592. [CrossRef]

47. Saber, W.I.; Ghoneem, K.M.; Al-Askar, A.A.; Rashad, Y.M.; Ali, A.A.; Rashad, E.M. Chitinase production by *Bacillus subtilis* ATCC 11774 and its effect on biocontrol of *Rhizoctonia* diseases of potato. *Acta Biol. Hung.* **2015**, *66*, 436–448. [CrossRef] [PubMed]

48. Guleria, S.; Walia, A.; Chauhan, A.; Shirkot, C.K. Molecular characterization of alkaline protease of *Bacillus amyloliquefaciens* SP1 involved in biocontrol of *Fusarium oxysporum*. *Int. J. Food Microbiol.* **2016**, *232*, 134–143. [CrossRef] [PubMed]

49. Gautam, S.; Chauhan, A.; Sharma, R.; Sehgal, R.; Shirkot, C.K. Potential of *Bacillus amyloliquefaciens* for biocontrol of bacterial canker of tomato incited by *Clavibacter michiganensis* ssp. *michiganensis. Microb. Pathog.* **2019**, *130*, 196–203. [CrossRef]

50. Douriet-Gámez, N.R.; Maldonado-Mendoza, I.E.; Ibarra-Laclette, E.; Blom, J.; Calderón-Vázquez, C.L. Genomic analysis of *Bacillus* sp. strain b25, a biocontrol agent of maize pathogen *Fusarium verticillioides*. *Curr. Microbiol.* **2018**, *75*, 247–255. [CrossRef]

51. Jiang, C.-H.; Liao, M.-J.; Wang, H.-K.; Zheng, M.-Z.; Xu, J.-J.; Guo, J.-H. *Bacillus velezensis* a potential and efficient biocontrol agent in control of pepper gray mold caused by *Botrytis cinerea*. *Biol. Control* **2018**, *126*, 147–157. [CrossRef]

52. Yu, X.; Ai, C.; Xin, L.; Zhou, G. The siderophore-producing bacterium, *Bacillus subtilis* CAS15, has a biocontrol effect on *Fusarium* wilt and promotes the growth of pepper. *Eur. J. Soil Biol.* **2011**, *47*, 138–145. [CrossRef]

53. Villa-Rodríguez, E.; Parra-Cota, F.; Castro-Longoria, E.; López-Cervantes, J.; de los Santos-Villalobos, S. *Bacillus subtilis* TE3: A promising biological control agent against *Bipolaris sorokiniana*, the causal agent of spot blotch in wheat (Triticum turgidum L. subsp. durum). *Biol. Control* **2019**, *132*, 135–143. [CrossRef]

54. Rathore, A.S.; Gupta, R.D. Chitinases from bacteria to human: Properties, applications, and future perspectives. *Enzyme Res.* **2015**, *2015*, 791907. [CrossRef]

55. Kumar, M.; Brar, A.; Yadav, M.; Chawade, A.; Vivekanand, V.; Pareek, N. Chitinases—Potential candidates for enhanced plant resistance towards fungal pathogens. *Agriculture* **2018**, *8*, 88. [CrossRef]

56. Weikert, T.; Niehues, A.; Cord-Landwehr, S.; Hellmann, M.J.; Moerschbacher, B.M. Reassessment of chitosanase substrate specificities and classification. *Nat. Commun.* **2017**, *8*, 1698. [CrossRef] [PubMed]

57. Choi, Y.J.; Kim, E.J.; Piao, Z.; Yun, Y.C.; Shin, Y.C. Purification and characterization of chitosanase from Bacillus sp. strain KCTC 0377BP and its application for the production of chitosan oligosaccharides. *Appl. Environ. Microbiol.* **2014**, *70*, 4522–4531. [CrossRef]

58. Seo, D.J.; Lee, J.H.; Song, Y.S.; Park, R.D.; Jung, W.J. Expression patterns of chitinase and chitosanase produced from Bacillus cereus in suppression of phytopathogen. *Microb. Pathog.* **2014**, *73*, 31–36. [CrossRef]

59. Suyotha, W.; Yano, S.; Wakayama, M. α-1,3-Glucanase: Present situation and prospect of research. *World J. Microbiol. Biotechnol.* **2016**, *32*, 30. [CrossRef] [PubMed]

60. Latgé, J.P. The cell wall: A carbohydrate armour for the fungal cell. *Mol. Microbiol.* **2007**, *66*, 279–290. [CrossRef] [PubMed]

61. Planas, A. Bacterial 1,3–1,4-beta-glucanases: Structure, function and protein engineering. *Biochim. Biophys. Acta Protein Struct. Molec. Enzyme* **2000**, *1543*, 361–382. [CrossRef]

62. Mardanova, A.M.; Hadieva, G.F.; Lutfullin, M.T.; Khilyas, I.V.; Minnullina, L.F.; Gilyazeva, A.G.; Bogomolnaya, L.M.; Sharipova, M.R. *Bacillus subtilis* strains with antifungal activity against the phytopathogenic fungi. *Agric. Sci.* **2017**, *8*, 1–20.

63. Abdallah, R.A.B.; Stedel, C.; Garagounis, C.; Nefzi, A.; Jabnoun-Khiareddine, H.; Papadopoulou, K.K.; Daami-Remadi, M. Involvement of lipopeptide antibiotics and chitinase genes and induction of host defense in suppression of *Fusarium* wilt by endophytic *Bacillus* spp. in tomato. *Crop Prot.* **2017**, *99*, 45–58. [CrossRef]

64. Islam, M.R.; Jeong, Y.T.; Lee, Y.S.; Song, C.H. Isolation and identification of antifungal compounds from *Bacillus subtilis* C9 inhibiting the growth of plant pathogenic fungi. *Mycobiology* **2012**, *40*, 59–66. [CrossRef]

65. Khan, A.; Singh, P.; Srivastava, A. Synthesis, nature and utility of universal iron chelator-siderophore: A review. *Microbiol. Res.* **2018**, *212–213*, 103–111. [CrossRef] [PubMed]

66. Saha, M.; Sarkar, S.; Sarkar, B.; Sharma, B.K.; Bhattacharjee, S.; Tribedi, P. Microbial siderophores and their potential applications: A review. *Environ. Sci. Pollut. Res. Int.* **2016**, *23*, 3984–3999. [CrossRef] [PubMed]

67. Ahmed, E.; Holmström, S.J. Siderophores in environmental research: Roles and applications. *Microb. Biotechnol.* **2014**, *7*, 196–208. [CrossRef] [PubMed]

68. Hertlein, G.; Müller, S.; Garcia-Gonzalez, E.; Poppinga, L.; Süssmuth, R.D.; Genersch, E. Production of the catechol type siderophore bacillibactin by the honey bee pathogen *Paenibacillus* larvae. *PLoS ONE* **2014**, *9*, e108272. [CrossRef] [PubMed]

69. Khan, A.; Doshi, H.V.; Thakur, M.C. *Bacillus* spp.: A Prolific Siderophore Producer. In *Bacilli and Agrobiotechnology*; Islam, M., Rahman, M., Pandey, P., Jha, C., Aeron, A., Eds.; Springer: Cham, Germany, 2016; pp. 309–323.

70. Bjelić, D.; Marinković, J.; Tintor, B.; Mrkovački, N. Antifungal and plant growth promoting activities of indigenous rhizobacteria isolated from maize (*Zea mays* L.) rhizosphere. *Commun. Soil Sci. Plant Anal.* **2018**, *49*, 88–98. [CrossRef]

71. Pieterse, C.M.; Zamioudis, C.; Berendsen, R.L.; Weller, D.M.; Van Wees, S.C.; Bakker, P.A. Induced systemic resistance by beneficial microbes. *Annu. Rev. Phytopathol.* **2014**, *52*, 347–375. [CrossRef]

72. Van Wees, S.C.; De Swart, E.A.; Van Pelt, J.A.; Van Loon, L.C.; Pieterse, C.M. Enhancement of induced disease resistance by simultaneous activation of salicylate- and jasmonate-dependent defense pathways in *Arabidopsis thaliana*. *Proc. Natl. Acad. Sci. USA* **2000**, *97*, 8711–8716. [CrossRef]

73. Li, C.; Hu, W.; Pan, B.; Liu, Y.; Yuan, S.; Ding, Y.; Li, R.; Zheng, X.; Shen, B.; Shen, Q. Rhizobacterium *Bacillus amyloliquefaciens* strain SQRT3-mediated induced systemic resistance controls bacterial wilt of tomato. *Pedosphere* **2017**, *27*, 1135–1146. [CrossRef]

74. Choudhary, D.K.; Johri, B.N. Interactions of *Bacillus* spp. and plants-with special reference to induced systemic resistance (ISR). *Microbiol. Res.* **2009**, *164*, 493–513. [CrossRef]

75. Niu, D.; Wang, X.; Wang, Y.; Song, X.; Wang, J.; Guo, J.; Zhao, H. *Bacillus cereus* AR156 activates PAMP-triggered immunity and induces a systemic acquired resistance through a NPR1-and SA-dependent signaling pathway. *Biochem. Biophys. Res. Commun.* **2016**, *469*, 120–125. [CrossRef]

76. Singh, S.K.; Pathak, R.; Choudhary, V. Plant Growth-Promoting Rhizobacteria-Mediated Acquired Systemic Resistance in Plants Against Pest and Diseases. In *Microbial-Mediated Induced Systemic Resistance in Plants*; Choudhary, D.K., Varma, A., Eds.; Springer: Singapore, 2016; pp. 125–134.

77. Kloepper, J.W.; Ryu, C.M.; Zhang, S. Induced systemic resistance and promotion of plant growth by *Bacillus* spp. *Phytopathology* **2004**, *94*, 1259–1266. [CrossRef] [PubMed]

78. Beris, D.; Theologidis, I.; Skandalis, N.; Vassilakos, N. *Bacillus amyloliquefaciens* strain MBI600 induces salicylic acid dependent resistance in tomato plants against Tomato spotted wilt virus and Potato virus Y. *Sci. Rep.* **2018**, *8*, 10320. [CrossRef]

79. Nie, P.; Li, X.; Wang, S.; Guo, J.; Zhao, H.; Niu, D. Induced systemic resistance against *Botrytis cinerea* by *Bacillus cereus* AR156 through a JA/ET- and NPR1-dependent signaling pathway and activates pamp-triggered immunity in Arabidopsis. *Front. Plant Sci.* **2017**, *8*, 238. [CrossRef]

80. Spaepen, S.; Vanderleyden, J.; Remans, R. Indole-3-acetic acid in microbial and microorganism-plant signalling. *FEMS Microbiol. Rev.* **2007**, *31*, 425–448. [CrossRef] [PubMed]

81. Choi, H.K.; Song, G.C.; Yi, H.S.; Ryu, C.M. Field evaluation of the bacterial volatile derivative 3-pentanol in priming for induced resistance in pepper. *J. Chem. Ecol.* **2014**, *40*, 882–892. [CrossRef] [PubMed]

82. Kildea, S.; Ransbortyn, V.; Khan, M.R.; Fagan, B.; Leonard, G.; Mullins, E.; Doohan, F.M. *Bacillus megaterium* shows potential for the biocontrol of septoria tritici blotch of wheat. *Biol. Control* **2008**, *47*, 37–45. [CrossRef]

83. Gond, S.K.; Bergen, M.S.; Torres, M.S.; White, J.F. Endophytic *Bacillus* spp. produce antifungal lipopeptides and induce host defence gene expression in maize. *Microbiol. Res.* **2015**, *172*, 79–87. [CrossRef]

84. Chowdappa, P.; Kumar, S.M.; Lakshmi, M.J.; Mohan, S.P.; Upreti, K.K. 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*, 109–117. [CrossRef]

85. Rais, A.; Jabeen, Z.; Shair, F.; Hafeez, F.Y.; Hassan, M.N. *Bacillus* spp., a bio-control agent enhances the activity of antioxidant defense enzymes in rice against *Pyricularia oryzae*. *PLoS ONE* **2017**, *12*, e0187412. [CrossRef]

86. Jayapala, N.; Mallikarjunaiah, N.; Puttaswamy, H.; Gavirangappa, H.; Ramachandrappa, N.S. Rhizobacteria *Bacillus* spp. induce resistance against anthracnose disease in chili (*Capsicum annuum* L.) through activating host defense response. *Egypt. J. Biol. Pest Control* **2019**, *29*, 45. [CrossRef]

87. Jain, S.; Vaishnav, A.; Kumari, S.; Varma, T.; Tuteja, N.; Kumar Choudhary, D. Chitinolytic *Bacillus*-mediated induction of jasmonic acid and defense-related proteins in soybean (*Glycine max* L. Merrill) plant against *Rhizoctonia solani* and *Fusarium oxysporum*. *J. Plant Growth Regul.* **2017**, *36*, 200–214. [CrossRef]

88. Chen, F.; Wang, M.; Zheng, Y.; Luo, J.; Yang, X.; Wang, X. Quantitative changes of plant defense enzymes and phytohormone in biocontrol of cucumber Fusarium wilt by *Bacillus subtilis* B579. *World J. Microbiol. Biotechnol.* **2010**, *26*, 675–684. [CrossRef]

89. Nandeeshkumar, P.; Ramachandrakini, K.; Prakash, H.S.; Niranjana, S.R.; Shekar Shetty, H. Induction of resistance against downy mildew on sunflower by rhizobacteria. *J. Plant Interact.* **2008**, *3*, 255–262. [CrossRef]

90. Cabello, P.; Roldán, M.D.; Castillo, F.; Moreno-Vivián, C. Nitrogen Cycle. In *Encyclopedia of Microbiology*; Schaechter, M., Ed.; Academic Press: London, UK, 2009; pp. 299–321.

91. Mus, F.; Crook, M.B.; Garcia, K.; Garcia Costas, A.; Geddes, B.A.; Kouri, E.D.; Paramasivan, P.; Ryu, M.-H.; Oldroyd, G.E.D.; Poole, P.S.; et al. Symbiotic nitrogen fixation and the challenges to its extension to nonlegumes. *Appl. Environ. Microbiol.* **2016**, *82*, 3698–3710. [CrossRef] [PubMed]

92. Rascio, N.; La Rocca, N. Biological Nitrogen Fixation. In *Encyclopedia of Ecology*; Fath, B., Ed.; Elsevier: Amsterdam, The Netherlands, 2013; pp. 264–279.

93. Kuan, K.B.; Othman, R.; Abdul Rahim, K.; Shamsuddin, Z.H. Plant growth-promoting rhizobacteria inoculation to enhance vegetative growth, nitrogen fixation and nitrogen remobilisation of maize under greenhouse conditions. *PLoS ONE* **2016**, *11*, e0152478. [CrossRef] [PubMed]

94. Ding, Y.; Wang, J.; Liu, Y.; Chen, S. Isolation and identification of nitrogen-fixing bacilli from plant rhizospheres in Beijing region. *J. Appl. Microbiol.* **2005**, *99*, 1271–1281. [CrossRef]

95. Xie, G.H.; Su, B.L.; Cui, Z.J. Isolation and identification of N2-fixing strains of Bacillus in rice rhizosphere of the Yangtze River valley. *Acta Microbiol. Sin.* **1998**, *38*, 480–483.

96. Szilagyi-Zecchin, V.J.; Ikeda, A.C.; Hungria, M.; Adamoski, D.; Kava-Cordeiro, V.K.; Glienke, C.; Galli-Terasawa, L.V. Identification and characterization of endophytic bacteria from corn (Zea mays L.) roots with biotechnological potential in agriculture. *AMB Express* **2014**, *4*, 1–9. [CrossRef]

97. Ikeda, S.; Tokida, T.; Nakamura, H.; Sakai, H.; Usui, Y.; Okubo, T.; Tago, K.; Hayashi, K.; Sekiyama, Y.; Ono, H.; et al. Characterization of leaf blade- and leaf sheath-associated bacterial communities and assessment of their responses to environmental changes in CO_2, temperature, and nitrogen levels under field conditions. *Microbes Environ.* **2015**, *30*, 51–62. [CrossRef]

98. Bahadir, P.S.; Liaqat, F.; Eltem, R. Plant growth promoting properties of phosphate solubilizing Bacillus species isolated from the Aegean Region of Turkey. *Turk. J. Bot.* **2018**, *42*, 1–14. [CrossRef]

99. Garcia-Lopez, A.M.; Delgado, A. Effect of *Bacillus subtilis* on phosphorus uptake by cucumber as affected by iron oxides and the solubility of the phosphorus source. *Agric. Food Sci.* **2016**, *25*, 216–224. [CrossRef]

100. Radhakrishnan, R.; Lee, I.J. Gibberellins producing *Bacillus methylotrophicus* KE2 supports plant growth and enhances nutritional metabolites and food values of lettuce. *Plant Physiol. Biochem.* **2016**, *109*, 181–189. [CrossRef] [PubMed]

101. Arkhipova, T.N.; Veselov, S.U.; Melentiev, A.I.; Martynenko, E.V.; Kudoyarova, G.R. Ability of bacterium Bacillus subtilis to produce cytokinins and to influence the growth and endogenous hormone content of lettuce plants. *Plant Soil* **2005**, *272*, 201–209. [CrossRef]

102. Ortíz-Castro, R.; Valencia-Cantero, E.; López-Bucio, J. Plant growth promotion by *Bacillus megaterium* involves cytokinin signaling. *Plant Signal. Behav.* **2008**, *3*, 263–265. [CrossRef]

103. Naz, I.; Bano, A.; Ul-Hassan, T. Isolation of phytohormones producing plant growth promoting rhizobacteria from weeds growing in Khewra salt range, Pakistan and their implication in providing salt tolerance to *Glycine max* L. *Afr. J. Biotechnol.* **2009**, *8*, 5762–5766.

104. Xu, M.; Sheng, J.; Chen, L.; Men, Y.; Gan, L.; Guo, S.; Shen, L. Bacterial community compositions of tomato (*Lycopersicum esculentum* Mill.) seeds and plant growth promoting activity of ACC deaminase producing *Bacillus subtilis* (HYT-12-1) on tomato seedlings. *World J. Microbiol. Biotechnol.* **2014**, *30*, 835–845. [CrossRef] [PubMed]

105. Park, Y.-G.; Mun, B.-G.; Kang, S.-M.; Hussain, A.; Shahzad, R.; Seo, C.-W.; Kim, A.-Y.; Lee, S.-U.; Oh, K.Y.; Lee, D.Y.; et al. *Bacillus aryabhattai* SRB02 tolerates oxidative and nitrosative stress and promotes the growth of soybean by modulating the production of phytohormones. *PLoS ONE* **2017**, *12*, e0173203. [CrossRef]

106. Shahzad, R.; Khan, A.L.; Bilal, S.; Waqas, M.; Kang, S.-M.; Lee, I.-J. Inoculation of abscisic acid-producing endophytic bacteria enhances salinity stress tolerance in *Oryza sativa*. *Environ. Exp. Bot.* **2017**, *136*, 68–77. [CrossRef]

107. Shen, J.; Yuan, L.; Zhang, J.; Li, H.; Bai, Z.; Chen, X.; Zhang, W.; Zhang, F. Phosphorus dynamics: From soil to plant. *Plant Physiol.* **2011**, *156*, 997–1005. [CrossRef]

108. Rodríguez, H.; Fraga, R. Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnol. Adv.* **1999**, *17*, 319–339. [CrossRef]

109. Granada, C.E.; Passaglia, L.; de Souza, E.M.; Sperotto, R.A. Is phosphate solubilization the forgotten child of plant growth-promoting rhizobacteria? *Front. Microbiol.* **2018**, *9*, 2054. [CrossRef]

110. Sharma, S.B.; Sayyed, R.Z.; Trivedi, M.H.; Gobi, T.A. Phosphate solubilizing microbes: Sustainable approach for managing phosphorus deficiency in agricultural soils. *Springerplus* **2013**, *2*, 587–600. [CrossRef] [PubMed]

111. Richardson, A.E.; Simpson, R.J. Soil microorganisms mediating phosphorus availability. *Plant Physiol.* **2011**, *156*, 989–996. [CrossRef]

112. Saeid, A.; Prochownik, E.; Dobrowolska-Iwanek, J. Phosphorus solubilization by Bacillus species. *Molecules* **2018**, *23*, 2897. [CrossRef]

113. Tao, G.C.; Tian, S.J.; Cai, M.Y.; Xie, G.H. Phosphate-solubilizing and -mineralizing abilities of bacteria isolated from soils. *Pedosphere* **2008**, *18*, 515–523. [CrossRef]

114. Woodward, A.W.; Bartel, B. Auxin: Regulation, action, and interaction. *Ann. Bot.* **2005**, *95*, 707–735. [CrossRef] [PubMed]

115. Khalid, A.; Arshad, M.; Zahir, Z.A. Screening plant growth promoting rhizobacteria for improving growth and yield of wheat. *J. Appl. Microbiol.* **2004**, *96*, 473–480. [CrossRef] [PubMed]

116. Bhutani, N.; Maheshwari, R.; Negi, M.; Suneja, P. Optimization of IAA production by endophytic *Bacillus* spp. from *Vigna radiata* for their potential use as plant growth promoters. *Isr. J. Plant Sci.* **2018**, *65*, 83–96. [CrossRef]

117. Ambreetha, S.; Chinnadurai, C.; Marimuthu, P.; Balachandar, D. Plant-associated *Bacillus* modulates the expression of auxin-responsive genes of rice and modifies the root architecture. *Rhizosphere* **2018**, *5*, 57–66. [CrossRef]

118. Gutierrez-Manero, F.J.; Ramos-Solano, B.; Probanza, A.; Mehouachi, J.R.; Tadeo, F.; Talon, M. The plant-growth-promoting rhizobacteria *Bacillus pumilus* and *Bacillus licheniformis* produce high amounts of physiologically active gibberellins. *Physiol. Plant* **2001**, *111*, 206–211. [CrossRef]

119. Barea, J.M.; Navaro, E.; Montoya, E. Production of plant growth regulators by rhizosphere phosphate-solubilizing bacteria. *J. Appl. Bacteriol.* **1976**, *40*, 129–134. [CrossRef]

120. Glick, B.R. Bacteria with ACC deaminase can promote plant growth and help to feed the world. *Microbiol. Res.* **2014**, *169*, 30–39. [CrossRef]

121. Gamalero, E.; Glick, B.R. Bacterial modulation of plant ethylene levels. *Plant Physiol.* **2015**, *169*, 13–22. [CrossRef]

122. Glick, B.R.; Todorovic, B.; Czarny, J.; Cheng, Z.; Duan, J.; McConkey, B. Promotion of plant growth by bacterial ACC deaminase. *Crit. Rev. Plant Sci.* **2007**, *26*, 227–242. [CrossRef]

123. Khan, A.L.; Halo, B.A.; Elyassi, A.; Ali, S.; Al-Hosni, K.; Hussain, J.; Al-Harrasi, A.; Lee, I.-J. Indole acetic acid and ACC deaminase from endophytic bacteria improves the growth of *Solanum lycopersicum*. *Electron. J. Biotechnol.* **2016**, *21*, 58–64.

124. Nascimento, F.X.; Rossi, M.J.; Soares, C.R.; McConkey, B.J.; Glick, B.R. New insights into 1-aminocyclopropane-1-carboxylate (ACC) deaminase phylogeny, evolution and ecological significance. *PLoS ONE* **2014**, *9*, e99168. [CrossRef] [PubMed]

125. Porwal, S.; Lal, S.; Cheema, S.; Kalia, V.C. Phylogeny in aid of the present and novel microbial lineages: Diversity in *Bacillus*. *PLoS ONE* **2009**, *4*, e4438. [CrossRef] [PubMed]

126. Sicuia, O.A.; Constantinscu, F.; Cornea, C.P. Biodiversity of *Bacillus subtilis* group and beneficial traits of *Bacillus* species useful in plant protection. *Rom. Biotechnol. Lett.* **2015**, *20*, 10737–10750.

127. Abedinzadeh, M.; Etesami, H.; Alikhani, H.A. Characterization of rhizosphere and endophytic bacteria from roots of maize (*Zea mays* L.) plant irrigated with wastewater with biotechnological potential in agriculture. *Biotechnol. Rep.* **2019**, *21*, e00305. [CrossRef]

128. Gao, S.; Wu, H.; Yu, X.; Qian, L.; Gao, X. Swarming motility plays the major role in migration during tomato root colonization by *Bacillus subtilis* SWR01. *Biol. Control.* **2016**, *98*, 11–17. [CrossRef]

129. Beauregard, P.B.; Chai, Y.R.; Vlamakis, H.; Losick, R.; Kolter, R. *Bacillus subtilis* biofilm induction by plant polysaccharides. *Proc. Natl. Acad. Sci. USA* **2013**, *110*, E1621–E1630. [CrossRef]

130. Zhang, N.; Yang, D.; Wang, D.; Miao, Y.; Shao, J.; Zhou, X.; Xu, Z.; Li, Q.; Feng, H.; Li, S.; et al. Whole transcriptomic analysis of the plant-beneficial rhizobacterium *Bacillus amyloliquefaciens* SQR9 during enhanced biofilm formation regulated by maize root exudates. *BMC Genom.* **2015**, *16*, 685. [CrossRef] [PubMed]

131. Martins, S.J.; Medeiros, F.H.V.; Lakshmanan, V.; Bais, H.P. Impact of seed exudates on growth and biofilm formation of *Bacillus amyloliquefaciens* ALB629 in common bean. *Front. Microbiol.* **2018**, *8*, 2631. [CrossRef] [PubMed]

132. Olanrewaju, O.S.; Ayangbenro, A.S.; Glick, B.R.; Babalola, O.O. Plant health: Feedback effect of root exudates-rhizobiome interactions. *Appl. Microbiol. Biotechnol.* **2019**, *103*, 1155–1166. [CrossRef] [PubMed]

133. Stamenkovic Stojanovic, S.; Karabegovic, I.; Beskoski, V.; Nikolic, N.; Lazic, M. *Bacillus* based microbial formulations: Optimization of the production process. *Hem. Ind.* **2019**, *73*, 169–182. [CrossRef]

134. Rosenberg, G.; Steinberg, N.; Oppenheimer-Shaanan, Y.; Olender, T.; Doron, S.; Ben-Ari, J.; Sirota-Madi, A.; Bloom-Ackermann, Z.; Kolodkin-Ga, I. Not so simple, not so subtle: The interspecies competition between *Bacillus simplex* and *Bacillus subtilis* and its impact on the evolution of biofilms. *NPJ Biofilms Microb.* **2016**, *2*, 15027. [CrossRef] [PubMed]

135. Monteiro, S.M.S.; Clemente, J.J.; Carrondo, M.J.T.; Cunha, A.E. Enhanced spore production of *Bacillus subtilis* grown in a chemically defined medium. *Adv. Microbiol.* **2014**, *4*, 444–454. [CrossRef]