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THE ROLE OF *BACILLUS* SPP. IN SUSTAINABLE AGRICULTURE AND BIOCONTROL

This *work* ***aims*** *to explore the potential applications of Bacillus spp. in biological plant control and the promotion of sustainable agriculture, drawing insights from an analysis of literature data.* ***Literature review.*** *Plants that interact with plant growth-promoting rhizobacteria (PGPR) exhibit improved growth and enhanced resistance to stress. Among PGPR, Bacillus spp. are widely used in agriculture to boost crop yields and stress tolerance. However, their effectiveness varies under different conditions, emphasizing the need for further research to bridge the gap between laboratory and field results. Species such as Bacillus subtilis enhance nitrogen fixation, facilitate phosphorus mobilization, and increase iron uptake in plants. Additionally, Bacillus spp. produce phytohormones and other compounds that regulate the hormonal balance in plants. These bacteria protect plants from pathogens by producing antimicrobial substances such as lipopeptides and antibiotics. B. subtilis also modulates the expression of plant genes to support colonization. Biofilm formation on plant roots, regulated by quorum sensing, further promotes effective bacterial colonization.* ***Conclusions.*** *Studies on plant-bacteria interactions in the rhizosphere reveal that beneficial bacteria like Bacillus spp. enhance plant growth and resilience through hormone regulation, biofilm formation, modulation of plant immune responses, and improved nutrient availability and stress tolerance. B. subtilis and related species are particularly effective in increasing crop yields and combating plant diseases. Their ability to improve drought and salt tolerance is especially noteworthy, making Bacillus spp. promising candidates for sustainable agriculture.*

Key words: Bacillus spp., plant growth promoting rhizobacteria, biocontrol, biofilm, sustainable agriculture.

Bacteria play a fundamental role in nutrient cycles, significantly influencing the carbon and nitrogen cycles and impacting daily life in both beneficial and harmful ways. Recent studies highlight that interactions with bacteria promote healthy development, while imbalances in the microbiome can lead to severe health issues [10].

The importance of plant-bacteria interactions has been recognized for over a century. Early discoveries revealed that the soil surrounding plant roots, known as the rhizosphere, harbors significantly higher bacterial populations

than adjacent bulk soil. This finding spurred extensive research into plant-associated bacteria [29]. Subsequent studies demonstrated that plants rely on symbiotic relationships with bacteria, including nitrogen-fixing species. Certain bacteria, classified as plant growth-promoting rhizobacteria (PGPR), have been shown to enhance the yields of critical crops such as soybeans and maize, as well as reduce the severity of plant diseases. PGPRs colonize the rhizosphere and plant roots, where they improve nutrient availability, mitigate abiotic stresses (e.g., drought or salinity), bolster plant defense mechanisms, and suppress pathogens. The advantages of PGPRs over traditional agrochemicals have driven the development of biological agricultural products. Biocontrol agents, such as PGPRs, are hypothesized to slow the evolution of resistant pathogens more effectively than conventional pesticides – a hypothesis that remains an active area of research [7]. Furthermore, biopesticides like PGPRs are widely regarded as more environmentally friendly alternatives to agrochemicals, which have caused significant environmental pollution over recent decades [11].

Bacillus subtilis is one of the most extensively researched and widely utilized plant growth-promoting rhizobacteria (PGPR), showing significant promise for agricultural applications. Members of the genus *Bacillus*, including *B. subtilis*, are frequently isolated from soil and have been identified in the rhizosphere of various plant species [51]. This Gram-positive, non-pathogenic bacterium has been extensively studied as a model organism for secondary metabolite production, sporulation, biofilm formation, and root adhesion [31]. Its ability to form resilient endospores provides exceptional resistance to abiotic stresses such as drought, extreme temperatures, and nutrient deficiencies, further enhancing its suitability for agricultural use. *B. subtilis* is already a key component in several commercial biological products, including *Serenade*, *Subtilex*, and *Cease* [9], underscoring its practical value in sustainable agriculture.

The rapid emergence of resistant plant pathogens outstrips the development of new pesticides, underscoring the substantial potential of biological products in agriculture [19, 59]. Despite over five decades of development and application, agriculture remains heavily reliant on traditional chemical methods. Although biological products have demonstrated efficacy in controlled environments, their performance in field conditions is often variable [3, 39]. For example, inoculation of canola with a commercial strain of *B. subtilis* significantly reduced the severity of *Plasmodiophora brassicae* disease by over 80% under controlled conditions, yet this effect was less pronounced in field trials. Similarly, strawberry leaf inoculations with *B. subtilis* showed a 50% reduction in biocontrol agent presence in the field after 8 days, in contrast to stable levels observed under controlled conditions [66]. These observations highlight the complexity of plant-bacteria interactions, particularly under unregulated conditions. A deeper understanding of these interactions could enable more effective and rational application of live bacteria in biological products.

B. subtilis employs both direct and indirect mechanisms to enhance plant growth and yield, including improved nutrient availability, modulation of plant hormone homeostasis, and alleviation of abiotic stress. *Bacillus* species secrete metabolites that promote plant growth and prevent pathogen infection [45].

Specifically, these bacteria assist plants in coping with ecological stresses, such as climate change, with *B. subtilis* playing a pivotal role in enhancing resilience to biotic stress [28]. This stress resistance involves the expression of specific genes and consequent synthesis of hormones, such as 1-aminocyclopropane-1-carboxylate deaminase (ACC). Ethylene, which restricts root and shoot growth, is regulated by bacterial ACC to mitigate plant stress and maintain normal growth. Additionally, *Bacillus* spp. secrete exopolysaccharides and siderophores that inhibit the movement of toxic ions, support ion balance, facilitate water transport within plant vessels, and suppress pathogen growth [45].

This work **aims** to explore the potential applications of *Bacillus* spp. in biological plant control and the promotion of sustainable agriculture, drawing insights from an analysis of literature data.

Nutrient mobilization and hormone regulation

Many essential nutrients and macro- and micronutrients, such as nitrogen, phosphorus, and iron, are present in the soil in forms that are not readily accessible to plants and must therefore be fixed or mobilized by rhizobacteria. For instance, plants cannot directly utilize atmospheric nitrogen and rely on microbial symbionts for this nutrient. *Bacillus subtilis* assists in nitrogen fixation and promotes nodule formation by other bacteria, enhancing the colonization of local symbiotic rhizobacteria. Phosphorus, another critical nutrient, also needs to be mobilized before it can be used by plants. *Bacillus subtilis* facilitates phosphorus solubilization through the production of various organic acids that convert it into a soluble form [47]. Additionally, metal ions such as iron often limit plant growth. Studies have shown that *B. subtilis* increases plant iron content by enhancing iron mobility through rhizosphere acidification and inducing the regulation of iron acquisition genes in plants [22].

Beyond nutrient mobilization, *B. subtilis* produces a range of compounds that directly influence plant growth. Notably, *B. subtilis* modulates plant hormone homeostasis, promoting cell division and plant growth either by producing growth hormones directly or by inducing their production in plants through secreted compounds.

Two volatile organic compounds produced by *B. subtilis*, namely 3-hydroxy-2-butanone (acetoin) and 2.3-butanediol, contribute to plant growth by altering cytokinin and ethylene homeostasis. The mixture of volatile compounds from *B. subtilis* can regulate auxin homeostasis in *Arabidopsis thaliana*, leading to reduced auxin levels in the leaves and increased levels in the roots. Since auxin inhibits leaf expansion but promotes root development, this redistribution may support optimal plant growth. Additionally, spermidine, a polyamine produced by *B. subtilis*, enhances plant growth by inducing expansins and reducing ethylene levels in plants. Both inoculation with producer strains and synthetic mixtures significantly improved root development [68].

In addition to such signaling molecules that indirectly affect hormone homeostasis, *B. subtilis* is also known to produce phytohormones [27]. Inoculation with a *B. subtilis* strain that produces cytokinin resulted in a substantial increase in cytokinin levels in lettuce plants, leading to improved growth and yield. This growth

stimulation effect is attributed to the uptake of cytokinin produced by *B. subtilis* by the roots rather than enhanced nutrient availability [7].

Enhancing drought and salt tolerance

Water scarcity and soil salinization are two major constraints in modern agriculture. Drought is one of the most severe environmental stressors affecting crop yields worldwide and is expected to intensify due to climate change in the near future. Freshwater is a limited resource, and irrigation for agricultural crops may decrease in the coming decades. Additionally, prolonged irrigation contributes to soil salinization, with approximately 20 to 50% of irrigated agricultural lands currently affected by salt contamination [20].

B. subtilis has been shown to enhance plant tolerance to drought and salt stress. Recent studies by Woo et al. [67] demonstrated that inoculation with *B. subtilis* strain GOT9 improves the drought and salt stress resistance of *Arabidopsis thaliana* and *Brassica campestris* through the modulation of plant gene expression, including the upregulation of genes involved in abscisic acid (ABA) biosynthesis, a key plant hormone for stress regulation. Furthermore, *B. subtilis* strain has been shown to increase osmotic stress tolerance in *A. thaliana*. In this context, the strain mitigates drought-induced damage by enhancing the biosynthesis of osmoprotectants in the plant and regulating the plant-specific Na+ importer HKT1 [7].

Biocontrol

Bacillus spp. are widely recognized as safe microorganisms that produce bioactive compounds beneficial for agricultural crops. Their ability to form endospores enables them to withstand adverse environmental conditions. In the rhizosphere, *Bacillus* spp. often function as endophytes, forming symbiotic relationships with plants and providing protection against pathogens. *B. subtilis* employs a range of direct and indirect mechanisms to safeguard plants, including the production of antimicrobial compounds and the activation of induced systemic resistance.

B. subtilis is known to produce over 24 antibiotic compounds [28]. These substances can be peptide-based, protein-based, or non-peptide-based, with non-peptide antibiotics classified as ribosomal or non-ribosomal peptide antibiotics [62].

Different *B. subtilis* strains synthesize a range of hydrolytic enzymes such as cellulases, proteases, and beta-glucanases, which adapt the surrounding environment to their benefit. These bacteria also produce exoenzymes that break down cell walls and various metabolites that can inhibit the growth or activity of other microorganisms. *B. subtilis* strains are known to synthesize antibiotic lipopeptides, including fengycin, surfactin, and iturin. Lipopeptides are low-molecular-weight compounds with surfactant properties, representing prominent examples of biosurfactants [37]. One of the most studied secondary metabolites of *B. subtilis* is surfactin, a cyclic acidic lipopeptide known for its diverse functions, including signal transduction and surface tension reduction. Due to its amphiphilic nature, surfactin can disrupt the cell membranes of other organisms by integrating into lipid layers. It is frequently reported as an active compound in the biocontrol

of plant pathogens by *B. subtilis* [17]. Surfactin is the most effective biosurfactant produced by *B. subtilis*, forming a hydrophobic globular structure in water and air [13, 49].

Inoculation with surfactin-producing *B. subtilis* significantly reduces the mortality of *Arabidopsis thaliana* infected with *Pseudomonas syringae*, an effect not observed with surfactin-deficient mutant strains. Additionally, surfactin inhibits *P. syringae* in liquid cultures at biologically relevant concentrations. Fan et al. [17] observed that surfactin-producing *B. subtilis* 9407 exhibits strong antibacterial activity *in vitro* against the pathogen *Acidovorax citrulli* and is highly effective in controlling melon seedling diseases in greenhouses. These abilities were lost in a surfactin-deficient mutant, highlighting the importance of surfactin in biocontrol [17]. However, surfactin-deficient mutants have shown other notable phenotypic changes that might reduce their biocontrol efficacy. Since surfactin production is closely linked with the synthesis of other antimicrobial secondary metabolites, these mutants may also lack other antimicrobial properties [33].

Most *B. subtilis* strains produce several antimicrobial compounds. Surfactin and bacilomycin act synergistically against pathogens, with their biosynthetic pathways being at least partially interconnected. Surfactin-deficient *B. subtilis* mutants do not produce bacilomycin, but the addition of exogenous surfactin restores its production. Bacilomycin-deficient mutants show reduced control over *Rhizoctonia solani* compared to wild-type strains [33].

Volatile compounds produced by *B. subtilis* can inhibit spore germination and hyphal growth of the phytopathogen *Botrytis cinerea* in an independent, non-contact manner on agar plates. However, the involvement of these volatiles in plant biocontrol remains unconfirmed.

Iturins are classified into iturins A, C, D, and E; mycosubtilin; bacilomycins D, F, and L; and bacilopcin [37]. Iturins exhibit antifungal and antimicrobial activities against yeasts and are considered excellent biopesticides.

Fengycins A, B, and C possess strong antifungal and antibacterial properties [62].

Bacillus subtilis produces peptide antibiotics known as bacteriocins, categorized into four classes based on their genetic and biochemical characteristics. Class I bacteriocins, or lantibiotics, are commonly used as antibiotics and are further classified into types A and B based on their antimicrobial activity and chemical structure.

B. subtilis mitigates disease severity not only through direct inhibition of pathogen growth but also by reducing pathogen virulence. This is partly due to its ability to interfere with quorum sensing (QS) signals, which regulate virulence gene expression. The enzyme AiiA produced by *B. subtilis* inactivates QS autoinducers. For instance, strain *B. subtilis* BS-1, which produces AiiA, reduces symptoms of soft rot in potatoes caused by *Erwinia carotovora*, a pathogen whose virulence is dependent on QS signals [7].

B. subtilis also competes directly with plant pathogens for resources, although experimental evidence supporting this mechanism remains limited. Indirect biocontrol strategies include biofilm formation, promotion of plant growth, competition for colonization sites, and the induction of systemic resistance (ISR)

[63]. Biofilm formation on plant roots plays a critical role in enhancing lipopeptide production, which significantly boosts antimicrobial activity in the surrounding soil. Notably, wild strains of *B. subtilis* demonstrate more robust biofilm formation compared to laboratory or commercial strains, underscoring their potential for biocontrol applications.

The genus *Bacillus* secretes various secondary metabolites that promote plant growth and enhance disease resistance. Studies indicate that *B. subtilis* can reduce the need for synthetic pesticides by promoting beneficial soil bacteria [40]. For example, *Bacillus thuringiensis* (Bt) and its toxins provide broad insecticidal control and support plant growth [3]. *B. cereus*, *B. amyloliquefaciens*, and *B. subtilis* are also effective against pests [23].

Lipopeptides produced by *Bacillus* inhibit the growth of phytopathogenic fungi like *Fusarium* spp., *Aspergillus* spp., and *Bipolaris sorokiniana*. These compounds show promise as biocontrol agents. For instance, lipopeptides from *B. subtilis* CMB32 significantly suppress anthracnose caused by *Colletotrichum gloeosporioides*. Additionally, biosurfactants from *Pseudomonas*, *Bacillus*, and *Acinetobacter* assist in heavy metal bioremediation and pesticide biodegradation. Nano-biofertilizers, incorporating *B. subtilis* and other beneficial microbes, enhance plant growth, limit fungal infections, and reduce the need for chemical fertilizers, thereby preventing groundwater contamination. Some volatile organic compounds (VOCs) released by *B. subtilis* (GB03) help plants recover from stress, while exopolysaccharides and siderophores from *Bacillus* species aid in maintaining ionic balance and suppressing pathogenic microbes [23].

Induced systemic resistance (ISR)

B. subtilis enhances plant defense by triggering induced systemic resistance (ISR), a process that strengthens the plant's overall resistance to a wide range of pathogens. This process involves ultra-structural and cytochemical changes in host cells in response to pathogen attack. *B. subtilis* activates ISR by forming colonies or biofilms in the rhizosphere, increasing host plant resistance to pathogens. Notably, ISR activation by *B. subtilis* leads to the synthesis of jasmonic acid (JA), ethylene, and the NPR1 regulatory gene [25].

ISR activation is associated with cell wall degradation, *de novo* production of glucanases and chitinases, and phytoalexin production related to disease resistance. For instance, *B. subtilis* (AUBS1) enhances the production of phenylalanine ammonia-lyase (PAL), peroxidase (POD), and *de novo* protein synthesis in rice leaves. Another strain, *B. subtilis* (UMAF6614), induces the secretion of salicylic acid (SA) and JA in melon plants, improving resistance to powdery mildew [25]. *B. subtilis* also boosts the synthesis of pathogenesis-related (PR) proteins in tobacco tissues, leading to increased resistance to mosaic virus, as evidenced by reduced mosaic symptoms in treated plants. Similarly, another *B. subtilis* strain reduces the activity of root-knot nematodes in tomato plants by activating ISR [1].

Inoculating roots with *B. subtilis* strains that naturally produce high levels of surfactin and fengycin can alleviate diseases caused by *Botrytis cinerea* in tomato and bean leaves. The absence of *B. subtilis* cells in the leaves suggests that disease reduction occurs through ISR. Moreover, strains with excessive surfactin

production significantly reduce disease symptoms compared to low-producer strains, indicating a correlation between ISR activation and surfactin levels [12].

B. subtilis inoculation in *Arabidopsis thaliana* triggers ISR by limiting the entry of *Pseudomonas syringae* pv. *tomato* DC3000 through stomata. Root colonization by *B. subtilis* significantly increases levels of ABA and salicylic acid, leading to stomatal closure and blocking infection [32]. Volatile compounds can also induce ISR. Airborne signals, when physically separating *Arabidopsis* seedlings from PGPR, significantly reduce symptomatic leaves after infection by *Erwinia carotovora*. These volatile compounds act independently of the signaling pathways used by PGPR in physical contact [7].

Root colonisation

B. subtilis forms thin biofilms on roots to facilitate long-term colonization of the rhizosphere. Chemotaxis enables the localization and colonization of young roots [2]. During the initial phase of root colonization, active and directed movement via chemotaxis is highly beneficial for plant growth-promoting rhizobacteria (PGPR) to anchor themselves to the roots [2]. Chemotaxis allows bacterial cells to sense changes in chemical gradients around them and move towards more favorable environments or away from toxins. The chemotactic response is initiated when stimulatory molecules bind to specific chemoreceptors located on the bacterial surface, leading to subsequent modification of CheA kinase and its response regulator, CheY [61]. CheY, in turn, interacts with the flagellar motor, controlling the direction of motor rotation and thus switching between swimming and tumbling [64]. In the absence of an attractant bound to the cognate chemoreceptor, CheA remains inactive and CheY is unphosphorylated, causing the flagellar motor to adopt a default clockwise rotation, leading the cell to reorient through tumbling. Upon attractant binding to the chemoreceptor, CheA becomes activated and subsequently phosphorylates CheY, resulting in counterclockwise rotation of the flagellar rotor and direct swimming towards the attractant. Less is known about how *B. subtilis* responds to repellents. It has been suggested that repellents act directly on the membrane rather than through the CheA-CheY pathway, leading to an increased frequency of tumbling [64].

Allard-Massicotte et al. [2] demonstrated that multiple chemoreceptors of *B. subtilis* are involved in the response to root exudates. A DcheA mutant, deficient in overall chemotaxis, and two non-motile mutants, a flagellar filament mutant Dhag and a flagellar motor mutant DmotA, were unable to colonize *A. thaliana* roots within 4 hours, unlike the wild-type (WT), indicating that chemotaxis is essential for root colonization. Additionally, they tested various chemoreceptor mutants in the presence of extracted root exudates in capillary assays, showing that chemoreceptors McpB, McpC, and to some extent TlpC are responsible for the response to amino acids and sugars present in the exudates. Notably, they also identified a mutant that exhibited significantly greater attraction to exudates compared to the WT, suggesting that the McpA chemoreceptor responds to a repellent molecule present in the exudates [2].

Studies have demonstrated that plants utilize the mechanism of root exudate secretion to actively attract desirable PGPR. Infection by the phytopathogen

Pseudomonas syringae induces the secretion of L-malic acid, which facilitates the colonization of *Bacillus subtilis* roots. Additionally, capillary assays have confirmed that L-malic acid can indeed elicit a chemotactic response in *B. subtilis* and may function as an attractant.

It has been proposed that the chemotactic response is specifically directed towards root exudates produced by individual plant species, suggesting that bacteria may have evolved to specifically respond to their encountered host plants [71]. Zhang and colleagues [71] demonstrated that a strain of *B. subtilis* isolated from the banana rhizosphere and a strain of *B. amylolicefaciens* isolated from the cucumber rhizosphere colonize their native host plants more effectively than other plants. They observed a higher chemotactic response of *B. subtilis* to concentrated banana root exudates compared to cucumber, which may explain the greater colonization of its original host plant [71].

Most publications on the role of chemotaxis in root colonization have investigated this process in liquid environments. In natural soil systems, entire clusters of cells move rapidly across solid surfaces as dynamic multicellular colonies, which may be of greater significance [24].

Unlike chemotactic swimming motility, swarming is non-directional and requires the production of surfactin, which reduces surface tension and forms a thin water film in which cells proliferate. Gao and colleagues [24] investigating cheA mutants, frequently used in chemotaxis studies, suggested that swarming might play an even more significant role in root colonization than chemotaxis. They examined a mutant with impaired chemotaxis, cheV, as well as three swarming mutants, namely srfAC, which are deficient in surfactin production, swrA, and minJ, each missing one of two genes from the swarming operon. They found that the chemotactic mutant could colonize with 80% efficiency, similar to the wild type (WT), whereas swarming mutants showed only 5–15% colonization efficiency. Additionally, the lack of surfactin may further affect root colonization, with swrA and minJ mutants displaying very elongated cells, suggesting other potential negative side effects [24].

The mechanism of chemotaxis encoded in bacterial genomes is unique to each bacterial species and is not related to genome size. Bacterial genomes contain multiple chemoreceptor genes along with genes regulating cell differentiation and their interactions with living organisms. The key role of bacterial chemoreceptors is to establish beneficial interactions between plants and bacteria. For instance, bacteria such as *Azotobacter chroococcum*, *Sinorhizobium meliloti*, *Pseudomonas*, and *Rhizobium* exhibit positive chemotaxis towards root exudates [65]. The genome of *B. subtilis* encodes 10 chemoreceptors, known as ligands, composed of amino acids, carbon, and oxygen, enabling this species to locate specific environments such as the rhizosphere [69]. *B. subtilis* plays a crucial role in this environment. *Bacillus* spp. require 24 hours to form a biofilm on plant roots. A biofilm is a multicellular bacterial community where cells are tightly connected and surrounded by a matrix they secrete. The timing of biofilm formation by *B. subtilis* on host plant roots also depends on the promoters of genes responsible for matrix secretion when the bacteria first encounter the root. Chemotactic signals required for *B. subtilis* colonization are activated 4–8 hours after inoculation [5].

Biofilm formation is more intense in wild strains of *B. subtilis* compared to laboratory or commercial strains. Ability to form a stable biofilm on plant roots is the significant advantage for the species. Biofilms are one of the most successful forms of life and are found across a wide range of environments [21]. They consist of cells closely packed together, embedded in an extracellular matrix (ECM), which in *B. subtilis* primarily consists of exopolysaccharide (EPS) and the protein TasA. Dragos and colleagues [14] demonstrated that both EPS and TasA are essential for successful root colonization. They reported that the number of cells colonizing the root was reduced in both EPS-deficient (Deps) and TasA-deficient (DtasA) mutants compared to the wild type (WT). Interestingly, when both mutants were inoculated on roots in a mixed culture, the ability to form a stable biofilm was restored, and the number of colonizing cells was actually significantly higher than in the WT, indicating that cells can share resources and distribute functions within *B. subtilis* biofilms on plant roots [14].

Mature biofilms of *B. subtilis* are known to be quite heterogeneous, and various phenotypes, aside from matrix producers, can be present even in monocultures, including competent, cannibalistic, digging, motile, and sporulating cells [35]. This specification of different tasks allows for functional distribution, thus ensuring efficient resource utilization that benefits the entire biofilm [58]. In *B. subtilis*, three main regulators have been identified as key elements in controlling cell differentiation: DegU for exoprotease secretion, ComA for competence and surfactin production, and Spo0A for matrix production and ultimately sporulation [35]. These regulators are activated during phosphorylation by specific kinases responding to external signals, including specific nutrients and signals from host plants, competitors, or collaborators [14, 41]. All three main regulators are important for root colonization to some extent.

The transition from swarming and chemotactic motility to biofilm formation is primarily initiated by the expression of the sinI gene, which is induced at intermediate levels of Spo0A~P. Deletion of the principal regulator Spo0A, as well as the matrix derepressor SinI, results in the inability of *Bacillus subtilis* to colonize the roots of *Arabidopsis thaliana*. Spo0A regulates the repression of matrix or motility genes through a double negative feedback loop involving SlrR and SinR. When Spo0A is unphosphorylated, sinI is not expressed, and SinR represses slrR, maintaining low levels of SlrR, which allows SinR to inhibit matrix genes, such as *eps* and *tasA*. At intermediate levels of Spo0A~P, this response regulator binds to the high-affinity site of sinI, activating the expression of SinI, which then binds to and inhibits SinR, leading to the derepression of slrR. The expressed SlrR, by forming a complex with SinR, inhibits SinR, resulting in prolonged SlrR expression. In this high SlrR state, the formation of SlrR-SinR complexes leads to low levels of free SinR, thereby derepressing matrix genes. Additionally, the SlrR-SinR complex suppresses the expression of the motility gene *hag* and the autolysin genes *lytABC* and *lytF*, resulting in the formation of stationary coherent cell chains that constitute the matrix. As Spo0A~P phosphorylation levels increase, other low-affinity operators of *sinI* bind, leading to decreased SinI production while sporulation genes are activated. Furthermore, the alternative matrix gene repressor AbrB, which also targets *eps, tasA,* and *blsA* (encoding a surface hydrophobicity

protein), is connected to the Spo0A pathway, providing additional fine-tuning of matrix-associated gene expression. AbrB is expressed at low levels of Spo0A~P and represses matrix genes, while intermediate levels of Spo0A~P cause repression of the *abrB* gene, simultaneously inducing the expression of AbbA, which inhibits the resident AbrB and thereby relieves repression of matrix genes [5, 60].

Key regulatory genes known to be essential for *in vitro* biofilm formation in *B. subtilis* are also important for effective root colonization and biocontrol against *Ralstonia solanacearum* in tomato plants. Various null mutations within the Spo0A pathways resulted in either hyper-strong biofilms with increased numbers of colonizing cells (*ΔabrB* and *ΔsinR*) or defective biofilms with reduced numbers of root-attached cells (*ΔsinI, Δeps,* and *ΔtasA*), depending on whether they positively or negatively impact biofilm development, respectively [7].

To date, five distinct kinases, from KinA to KinE, have been identified as initiating the Spo0A phosphorylation cascade in response to various signals. KinC and KinD have been found to play a direct role in root colonization by initiating biofilm formation in response to different plant signals. The *ΔkinD* mutant was unable to form a biofilm on tomato roots. It was determined that L-malic acid is the responsible signal for biofilm induction; however, since the concentrations required for biofilm formation were quite high, it was suspected that L-malic acid might primarily function as a carbon source, altering metabolism to favor biofilm existence. The combination of glycerol, a primary root exudate, and manganese strongly promotes biofilm formation. However, this effect was significantly reduced for *ΔkinD* and less so for the *ΔkinC* mutant, further indicating the importance of these kinases in biofilm formation in response to plant-related signals. Providing additional evidence that KinC and KinD are involved in biofilm formation in response to root exudates, Beauregard et al. [5] observed that plant polysaccharides such as arabinogalactan, pectin, and xylan induce the formation of a pellicle in *Bacillus subtilis*. They tested the ability of mutants deficient in each of the five kinases, from KinA to KinE, as well as the double mutant *ΔkinCD*, to form a pellicle in response to three plant polysaccharides, identifying KinC and KinD as sensors responsible for pectin and arabinogalactan. However, all mutants were still able to form a biofilm in response to xylan, suggesting the presence of an additional, yet unidentified pathway capable of initiating biofilm formation in response to plant signals. Furthermore, they identified over 40 predicted glycosylhydrolases in *B. subtilis* that could degrade plant polysaccharides, allowing their use as a carbon source for cell growth and other metabolic processes. Indeed, they demonstrated that *B. subtilis* utilizes plant polysaccharides to incorporate them into the matrix EPS [5].

In addition to Spo0A, DegU plays a crucial role in regulating the transition from motility to biofilm formation in *B. subtilis* by repressing motility genes in its phosphorylated form. It also regulates the production of the surface hydrophobic protein BslA and poly-γ-glutamic acid (PGA), which are important for stable biofilm formation [34, 70]. Yu et al. [70] observed that root colonization efficiency positively correlates with γ-PGA production in high-producing strains of *B. subtilis*. Although a direct link between root colonization and DegU in *B. subtilis* has not yet been demonstrated, the *ΔdegU* mutant of the closely related *B. amyloliquefaciens*

was unable to colonize *Arabidopsis thaliana* roots compared to the wild type, suggesting that DegU may be critical for root colonization [70].

The ultimate master regulator, ComA, influences root colonization by indirectly affecting biofilm formation. ComA also regulates surfactin production. Surfactin is considered a crucial signaling molecule that stimulates biofilm formation in *B. subtilis* by inducing potassium leakage. Surfactin-deficient mutants also exhibited disrupted biofilm formation, but only under conditions that do not naturally induce biofilm formation. In contrast, under biofilm-inducing conditions provided by media such as MSgg and MSNg, *B. subtilis* was able to form stable biofilms independent of surfactin. Moreover, no significant difference in root colonization ability was observed between the surfactin-deficient mutant (srfAA) and the wild type, indicating that surfactin is not essential for root colonization [55].

For further cellular differentiation, all three main regulators are additionally controlled via *quorum sensing* (QS) [42]. QS facilitates cell-to-cell communication based on the production, secretion, and response to autoinducers. This allows cells to detect the density of neighboring producers and potential collaborators and respond accordingly. QS is critical for the development of cooperative behaviors, as it regulates the synthesis of substances such as surfactin or ECM components. In *B. subtilis*, regulatory peptides (Phr) and their related response regulators, the aspartyl-phosphatases (Rap), mediate QS, which in turn regulates the activity of the three main regulators [42]. The autoinducer Phr is translated from pre-Phr proteins, which are secreted and processed into mature Phr peptides. At high cell densities, Phr peptides reach a threshold concentration that allows their import into the cell, where they bind to their corresponding Rap phosphatase and inhibit it. This alleviates the inhibition of the master regulator, leading to altered expression of target genes. Spo0A is regulated by RapABEHIJ60, as these phosphatases inhibit Spo0A phosphorylation by dephosphorylating Spo0F~P. In contrast, Rap phosphatases regulate ComA (RapCDFGHKPQ60) and DegU (RapG), primarily by preventing their DNA-binding activity [8, 69]. The extent to which QS plays a role in root colonization by *B. subtilis* remains unknown.

In addition to the QS autoinducer Phr and the secondary metabolite surfactin, *B. subtilis* produces and secretes cyclic di-adenosine monophosphate (c-di-AMP), which may function as a signal during biofilm formation. c-di-AMP acts as an extracellular signaling molecule, influencing biofilm formation and root colonization, potentially through changes in the phosphorylation state of Spo0A. However, the precise molecular mechanism remains to be elucidated [56].

The signaling responsible for inducing biofilm formation on roots is not a unidirectional process from plant to microbe, but rather an interaction between both parties. In addition to the compounds produced by plants that elicit chemotactic responses and biofilm formation in bacterial cells, *B. subtilis* is capable of affecting gene expression in plants, thereby promoting root colonization. Approximately 300 genes are differentially expressed in *Arabidopsis thaliana* when colonized by *B. subtilis*. This includes downregulation of genes associated with protective signaling in roots, as well as genes related to cell wall metabolism, which could contribute to both initial attachment and survival, thus facilitating overall root colonization. Indeed, suppression of genes involved in the plant's innate immune

response may play a crucial role during *B. subtilis* colonization of roots, as it may help bacterial cells evade the plant's defense mechanisms during initial colonization [46]. Various compounds produced by *B. subtilis*, including lipopeptides such as surfactins and iturins, as well as key bacterial components like flagellin, act as microbe-associated molecular patterns that trigger specific immune responses in plants [18]. Rekha et al. [46] observed that *B. subtilis* strain RR4 initially suppresses various immunity-related genes during root colonization of rice, thus aiding its own colonization, and subsequently induces defense responses to enhance plant immunity. Deng et al. [15] described how the endophyte *B. subtilis* strain BSn5 can mask its own-produced flagellin by producing the lantibiotic subtilomycin, thereby reducing the stimulation of the plant's defensive response.

It is suggested that the EXLX1 protein, produced and secreted by *Bacillus subtilis*, plays a crucial role in plant-microbe interactions. This protein has a structure highly similar to that of plant β-expansins, which are known to bind to plant cell walls and facilitate their expansion. Mutants deficient in EXLX1 production also showed a significant reduction in root colonization compared to wild-type strains [7].

Similar to how different *B. subtilis* strains vary in their ability to promote plant growth and control phytopathogens, they also differ in their capacity to successfully colonize plant roots. The genetic relatedness among different *B. subtilis* strains influences their ability to either co-colonize plant roots or competitively exclude each other. After inoculating *Arabidopsis thaliana* roots with multiple unrelated strains, the resulting biofilm on the roots predominantly consisted of a single strain, indicating an antagonistic interaction among the strains. In contrast, inoculation with pairs of related strains led to the formation of mixed biofilms and joint colonization, suggesting that *B. subtilis* colonizes plant roots in a manner that reflects genetic relatedness [53].

Interactions of *Bacillus* and plants

The potential of *B. subtilis* to promote plant growth and enhance plant defense against pathogens varies significantly among strains. While some compounds, particularly those with broad target ranges and multiple functions such as surfactin, are commonly synthesized by *B. subtilis* strains, the production of others, like subtilin, appears to be strain-specific [30]. This suggests that certain compounds may provide specific strains of *B. subtilis* with advantages in particular ecological niches, thereby helping to tailor and optimize plant-microbe interactions. It is evident that plant growth promotion and pathogen control are not unilaterally beneficial acts by *B. subtilis*. The bacteria also derive benefits from their interaction with plants. PGPR rely on carbon sources exuded by plants in nutrient-poor soils and often respond specifically to plant-produced signals [48]. Root exudates serve not only as a nutrient source for PGPR but also as signaling molecules that establish connections and initiate the colonization process [5]. Although some beneficial interactions between plants and microorganisms seem independent of direct physical contact, such as with volatile organic compounds, biocontrol and growth stimulation effects are heavily dependent on the PGPR's ability to effectively attach to and colonize the host plant, particularly under natural conditions. This highlights

the fundamental role of successful root colonization in bacterial interactions. In this context, several bacterial traits are important, including chemotaxis to sense and reach the plant root and biofilm formation for attachment and resilience on the root [27].

Growth promotion and pathogen suppression are achieved through the synthesis of various defensive compounds in host plant tissues, leading to ISR, which is supported by bacteria through antibiosis against pathogens. Additionally, bacteria can secrete phytohormones and other beneficial compounds. Soil particles bound by roots are easily colonized by bacteria, which compete with resident bacteria for rhizosphere nutrients. Thus, mutualism between bacteria develops through metabolic exchanges: plants provide organic substances (carbon) to resident bacteria, and in return, bacteria assist plants in absorbing water and nutrients from the soil. ISR induction and improved plant growth are additional outcomes of the mutualistic interaction between plants and bacteria [26]. *B. subtilis* plays a significant role among growth-promoting bacteria and in biocontrol. The advantage of using *B. subtilis* is its ability to activate ISR, likely mediated by salicylic acid. *B. subtilis* can be used to induce resistance by synthesizing protective enzymes in the host, such as POD, PPO, and PAL. In the event of pathogen attack, plants activate defensive mechanisms. This protective response often leads to systemic acquired resistance (SAR) and the induction of hypersensitive responses, resulting in the formation of brown, desiccated tissue. Inoculation of plants with *Bacillus subtilis* strain (pf4) resulted in high levels of SAR. Compared to non-inoculated plants, inoculated plants showed significantly higher similarity (96.5%), shoot length (9.0 cm), root length (8.03 cm), and strength index (1703). Treatment of sunflower seeds with *Pseudomonas fluorescens* enhanced root biomass production. Similar results were observed in castor bean seeds inoculated with *P. fluorescens* and *B. subtilis*, with a greater increase in growth achieved with *P. fluorescens* than with *B. subtilis*. When tomato seeds were treated with *Bacillus subtilis* (EPC016), a significant increase in seedling growth was observed compared to non-inoculated plants [28].

Most studies on *B. subtilis* root colonization have been conducted under sterile and strictly controlled conditions, which are far from the natural, complex environment of the plant rhizosphere and root. Laboratory observations are often difficult to reproduce in field conditions. The rhizosphere is shown to contain up to 10^{11} microbial cells per gram, representing over 30,000 species [6]. One reason for the variability in biocontrol success in field conditions may be natural plant microbiomes. Interactions among microbes can be either cooperative or competitive, meaning that depending on the bacterial community encountered, *B. subtilis* root colonization can be enhanced, reduced, or even successful or unsuccessful. For example, *Pseudomonas protegens*, another widely used PGPR, can inhibit *B. subtilis* biofilm formation in co-cultivation by producing a compound, 2.4-diacetylphloroglucinol, which delays cell differentiation by suppressing biofilm-specific genes [43]. Accordingly, biofilm formation not only plays a crucial role in root colonization but also modulates interactions with co-occurring microbes. Molina-Santiago et al. [38] noted that the *B. subtilis* D-matrix mutant, deficient

in biofilm matrix production, showed increased susceptibility to *Pseudomonas chlororaphis* invasion, leading to higher sporulation during co-inoculation of melon seeds. Conversely, co-inoculation of *B. subtilis* and *B. licheniformis* synergistically improved growth in red pepper and tomato plants, indicating a positive interaction between the pair.

It has been shown that adding *B. subtilis* to the natural rhizosphere has only a minor impact on the overall plant microbiome. Inoculation of tomato plants with *B. subtilis* in greenhouse studies affected the eukaryotic microbiome for 14 days, while the bacterial impact lasted only 3 days [44]. Wei et al. [66] observed a similar outcome for *B. subtilis* applied to leaves rather than root inoculation. Here, *B. subtilis* also appeared to have only a minor effect on the natural phyllosphere microbiome [66]. However, the impact of the natural plant microbiome on *B. subtilis* and whether specific taxa can enhance its root colonization remains unknown and needs further investigation.

Plant microbiome formation is largely determined by complex interactions between microorganisms [57]. Synergistic interactions and co-cultivation of multispecies biofilms of *Pseudomonas spp.* and *Bacillus spp.* on banana roots influenced colony composition at the root-microbiome interface and acted as a beneficial plant consortium against pathogens [54].

Synergetic interactions between nodule bacteria and *B. subtilis*

Disease suppression and stimulation of plant growth have been observed for the interaction between nodulating bacteria and *Bacillus subtilis*, which could stimulate the synthesis of phytohormones in host plants and in free-living, endophytic, rhizospheric, and symbiotic microorganisms present in the root system [50].

Various bacterial genera colonize the rhizosphere, including *Bacillus*, *Acinetobacter*, *Arthrobacter*, *Enterobacter*, *Cellulosimicrobium*, *Mycobacterium*, *Pseudomonas*, *Sinorhizobium* [16, 52]. Combined application of these bacteria results in enhanced plant growth stimulation, increased enzyme and antioxidant production, phosphorus solubilization, biocontrol activity, nodule formation, and nitrogen fixation.

B. subtilis demonstrates significant potential as a plant growth promoter and biocontrol agent. However, its effectiveness is influenced by environmental conditions and competition with other microorganisms. Despite its proven benefits, the variability observed in field performance underscores the need for further research to optimize its application and identify new strains with enhanced efficacy [28].

Conclusions. Studies on plant-bacteria interactions in the rhizosphere reveal that beneficial bacteria like *Bacillus* spp. enhance plant growth and resilience through hormone regulation, biofilm formation, modulation of plant immune responses, and improved nutrient availability and stress tolerance. *B. subtilis* and related species are particularly effective in increasing crop yields and combating plant diseases. Their ability to improve drought and salt tolerance is especially noteworthy, making *Bacillus* spp. promising candidates for sustainable agriculture.

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РОЛЬ *BACILLUS* SPP. У СТАЛОМУ ЗЕМЛЕРОБСТВІ ТА БІОКОНТРОЛІ

Реферат

Метою *даної роботи є аналіз літератури щодо потенційного використання Bacillus spp. у біологічному контролі рослин та розвитку сталого землеробства.* ***Огляд літератури.*** *Рослини, які взаємодіють із PGPR (ризобактеріями, що стимулюють ріст рослин), краще розвиваються і є більш стійкими до стресу. Bacillus spp. використовуються у сільському господарстві як PGPR для підвищення врожайності та стресостійкості культур, проте ефективність їх використання може змінюватися за різних умов. Відмінності у результатах випробувань між лабораторними і польовими умовами підкреслюють необхідність подальших досліджень у цій сфері. Bacillus spp., наприклад, B. subtilis, покращують фіксацію азоту, беруть участь у мобілізації фосфору та збільшують вміст заліза в рослинах. Крім того, Bacillus spp. виробляють фітогормони та сполуки, які регулюють гормональний баланс рослин. Бацили захищають рослини від патогенів, виробляючи антимікробні сполуки, такі як ліпопептиди та антибіотики. З метою кращої колонізації B. subtilis модулюють експресію генів рослин і утворюють біоплівки у процесі, що регулюється системою quorum sensing.* ***Висновки.*** *Дослідження взаємодії рослин і бактерій у ризосфері показали, що корисні бактерії, такі як Bacillus spp., покращують ріст і стійкість рослин шляхом регуляції гормонів, утворення біоплівок, впливу на імунні відповіді рослин, покращення доступності поживних речовин і стійкості до стресу. B. subtilis та інші види бацил є особливо ефективними у підвищенні врожайності культур та зменшенні захворюваності. Особливо важливою є їх здатність підвищувати стійкість рослин до посухи та солоності. Ці характеристики роблять Bacilli spp. перспективними та цінними для використання у сталому сільському господарстві.*

Ключові слова: Bacillus spp., ризобактерії. біоконтроль, біоплівка, стале землеробство.

СПИСОК ВИКОРИСТАНОЇ ЛІТЕРАТУРИ

1. *Adam M., Heuer H., Hallmann J.* Bacterial antagonists of fungal pathogens also control root-knot nematodes by induced systemic resistance of tomato plants // PLoS One. – 2014. – 9, № 2. – e90402. https://doi.org/10.1371/journal.pone.0090402
2. *Allard-Massicotte R., Tessier L., Lecuyer F., Lakshmanan V., Lucier J.F., Garneau D., Caudwell L., Vlamakis H., Bais H.P., Beauregard P.B. Bacillus subtilis* early colonization of *Arabidopsis thaliana* roots involves multiple chemotaxis receptors // MBio. – 2016. – 7, № 6. – e01664-16. doi: 10.1128/mBio.01664-16.

3. *Arrizubieta M., Simón O., Williams T., Caballero P.* Determinant factors in the production of a co-occluded binary mixture of *Helicoverpa armigera* alphabaculovirus (HearNPV) genotypes with desirable insecticidal characteristics // PLoS One. – 2016. – 11, № 10: e0164486. https://doi.org/10.1371/journal.pone.0164486
4. *Bardin M., Ajouz S., Comby M., Lopez-Ferber M., Graillot B., Siegwart M., Nicot P.C.* Is the efficacy of biological control against plant diseases likely to be more durable than that of chemical pesticides? // Front Plant Sci. – 2015. – 6:566. DOI: 10.3389/fpls.2015.00566
5. *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, № 17. – E1621-E1630. DOI: 10.1073/pnas.1218984110
6. *Berendsen R.L., Pieterse C.M., Bakker P.A.* The rhizosphere microbiome and plant health // Trends Plant Sci. – 2012. – 17, № 8. – P. 478–486. DOI: 10.1016/j.tplants.2012.04.001
7. *Blake C., Christensen M.N., Kovács Á.T.* Molecular aspects of plant growth promotion and protection by *Bacillus subtilis* // Mol Plant Microbe Interact. – 2021. – 34, № 1. – P. 15–25. doi: 10.1094/MPMI-08-20-0225-CR.
8. *Boguslawski K.M., Hill P.A., Griffith K.L.* Novel mechanisms of controlling the activities of the transcription factors Spo0A and ComA by the plasmid-encoded quorum sensing regulators Rap60-Phr60 in *Bacillus subtilis* // Mol Microbiol. – 2015. – 96, № 2. – P. 325–348. DOI: 10.1111/mmi.12939
9. *Borriss R. Bacillus*, a plant-beneficial bacterium. In: Lugtenberg B., editor. Principles of plant-microbe interactions. – Springer International Publishing; 2015. – P. 379–391. DOI: 10.1007/978-3-319-08574-6
10. *Bull M.J., Plummer N.T.* Part 1: The human gut microbiome in health and disease // Integr Med (Encinitas). – 2014. – 13, № 6. – P. 17–22. https://pubmed.ncbi.nlm.nih.gov/26770121/
11. *Carvalho F.P.* Pesticides, environment, and food safety // Food Energy Secur. – 2017. – 6, № 2. – P. 48–60. DOI: 10.1002/fes3.108
12. *Cawoy H., Mariutto M., Henry G., Fisher C., Vasilyeva N., Thonart P., Dommes J., Ongena M.* Plant defense stimulation by natural isolates of *Bacillus* depends on efficient surfactin production // Mol Plant Microbe Interact. – 2014. – 27, № 1. – P. 87–100. DOI: 10.1094/MPMI-09-13-0262-R
13. *Chen W.C., Juang R.S., Wei Y.H.* Applications of a lipopeptide biosurfactant, surfactin, produced by microorganisms // Biochem Eng J. – 2015. – 103. – P. 158–169. DOI: 10.1016/j.bej.2015.07.009
14. *Dragos A., Kiesewalter H., Martin M., Hsu C.Y., Hartmann R., Wechsler T., Eriksen C., Brix S., Drescher K., Stanley-Wall N., Kummerli R., Kovács Á.T.* Division of labor during biofilm matrix production // Curr Biol. – 2018. – 28, № 12. – P. 1903–1913.e5. DOI: 10.1016/j.cub.2018.04.046
15. *Deng Y., Chen H., Li C., Xu J., Qi Q., Xu Y., Zhu Y., Zheng J., Peng D., Ruan L., Sun M.* Endophyte *Bacillus subtilis* evade plant defense by producing lantibiotic subtilomycin to mask self-produced flagellin // Commun Biol. – 2019. – 2, № 368. DOI https://doi.org/10.1038/s42003-019-0614-0

16. *Egamberdieva D., Wirth S., Behrendt U., Abd_Allah E.F., Berg G.* Biochar treatment resulted in a combined effect on soybean growth promotion and a shift in plant growth promoting rhizobacteria // Front Microbiol. – 2016. – 7, № 209. https://doi.org/10.3389/fmicb.2016.00209
17. *Fan H., Zhang Z., Li Y., Zhang X., Duan Y., Wang Q.* Biocontrol of bacterial fruit blotch by *Bacillus subtilis* 9407 via surfactin-mediated antibacterial activity and colonization // Front Microbiol. – 2017. – 8, № 1973. https://doi.org/10.3389/fmicb.2017.01973
18. *Farace G., Fernandez O., Jacquens L., Coutte F., Krier F., Jacques P., Clément C., Barka E.A., Jacquard C., Dorey S.* Cyclic lipopeptides from *Bacillus subtilis* activate distinct patterns of defence responses in grapevine // Mol Plant Pathol. – 2015. – 16, № 2. – P. 177–187. doi: 10.1111/mpp.12170
19. *Fisher M.C., Hawkins N.J., Sanglard D., Gurr S.J.* Worldwide emergence of resistance to antifungal drugs challenges human health and food security // Science. – 2018. – 360, № 6390. – P. 739–742. DOI: 10.1126/science.aap7999
20. *Fita A., Rodriguez-Burruezo A., Boscaiu M., Prohens J., Vicente O.* Breeding and domesticating crops adapted to drought and salinity: A new paradigm for increasing food production // Front Plant Sci. – 2018. – 6, № 978. https://doi.org/10.3389/fpls.2015.00978
21. *Flemming H.C., Wingender J., Szewzyk U., Steinberg P., Rice S.A., Kjelleberg S.* Biofilms: An emergent form of bacterial life // Nat Rev Microbiol. – 2016. – 14, № 9. – P. 563–575. DOI: 10.1038/nrmicro.2016.94
22. *Freitas M.A., Medeiros F.H., Carvalho S.P., Guilherme L.R., Teixeira W.D., Zhang H., Pare P.W.* Augmenting iron accumulation in cassava by the beneficial soil bacterium *Bacillus subtilis* (GBO3) // Front Plant Sci. – 2015. – 6, № 596. https://doi.org/10.3389/fpls.2015.00596
23. *Gadhave K.R., Finch P., Gibson T.M., Gange A.C.* Plant growth-promoting *Bacillus* suppress *Brevicoryne brassicae* feld infestation and trigger density-dependent and density-independent natural enemy responses // J Pest Sci. – 2016. – 89, № 4. – P. 985–992. DOI: 10.1007/s10340-015-0721-8
24. *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. – P. 11–17. DOI: 10.1016/j.biocontrol.2016.03.011
25. *García-Gutiérrez M.S., Ortega-Álvaro A., Busquets-García A., Pérez-Ortiz J.M., Caltana L., Ricatti M.J., Manzanares J.* Synaptic plasticity alterations associated with memory impairment induced by deletion of CB2 cannabinoid receptors // Neuropharmacology. – 2013. – 73. – P. 388–396. DOI: 10.1016/j.neuropharm.2013.05.034
26. *Gouda S., Kerry R.G., Das G., Paramithiotis S., Shin H.S., Patra J.K.* Revitalization of plant growth promoting rhizobacteria for sustainable development in agriculture // Microbiol Res. – 2018. – 206. – P. 131–140. DOI: 10.1016/j.micres.2017.08.016
27. *Großkinsky D.K., Tafner R., Moreno M.V., Stenglein S.A., De Salamone I.E.G., Nelson L.M., Roitsch T.* Cytokinin production by *Pseudomonas fluorescens*

G20-18 determines biocontrol activity against *Pseudomonas syringae* in *Arabidopsis* // Sci Rep. – 2016. – 6, № 23310. DOI: 10.1038/srep23310
28. *Hashem A., Tabassum B., Abd_Allah E.F. Bacillus subtilis*: A plant-growth promoting rhizobacterium that also impacts biotic stress // Saudi J Biol Sci. – 2019. – 26, № 6. – P. 1291–1297. doi: 10.1016/j.sjbs.2019.05.004.
29. *Hiltner L.* Über neuere Erfahrungen und Probleme auf dem Gebiet der Bodenbakteriologie und unter besonderer Berücksichtigung der Gründüngung und Brache // Arbeit. Deut. Landw. Ges. Berl. – 1904. – 98. – P. 59–78. DOI: 10.12691/aees-1-6-1
30. *Kiesewalter H.T., Andrade C.N.L., Wibowo M., Strube M.L., Maroti G., Snyder D., Jørgensen T.S., Larsen T.O., Cooper V.S., Weber T., Kovács Á.T.* Genomic and chemical diversity of *Bacillus subtilis* secondary metabolites against plant pathogenic fungi // mSystems. – 2021. – 6, № 1. doi: 10.1101/2020.08.05.238063.
31. *Kovács Á.T. Bacillus subtilis* // Trends Microbiol. – 2019. – 27, № 9. – P. 724–725. DOI: 10.1016/j.tim.2019.03.008
32. *Kumar A.S., Lakshmanan V., Caplan J.L., Powell D., Czymmek K.J., Levia D.F., Bais H.P.* Rhizobacteria *Bacillus subtilis* restricts foliar pathogen entry through stomata // Plant J. – 2012. – 72. – P. 694–706. DOI: 10.1111/j.1365-313X.2012.05116.x
33. *Luo C., Zhou H., Zou J., Wang X., Zhang R., Xiang Y., Chen Z.* Bacillomycin L and surfactin contribute synergistically to the phenotypic features of *Bacillus subtilis* 916 and the biocontrol of rice sheath blight induced by *Rhizoctonia solani* // Appl Microbiol Biotechnol. – 2015. – 99. – P. 1897–1910. DOI: 10.1007/s00253-014-6195-4
34. *Marlow V.L., Porter M., Hobley L., Kiley T.B., Swedlow J.R., Davidson F.A., Stanley-Wall N.R.* Phosphorylated DegU manipulates cell fate differentiation in the *Bacillus subtilis* biofilm // J Bacteriol. – 2014. – 196, № 1. – P. 16–27. DOI: 10.1128/JB.00930-13
35. *Mielich-Süss B., Lopez D.* Molecular mechanisms involved in *Bacillus subtilis* biofilm formation // Environ Microbiol. – 2015. – 17, № 3. – P. 555–565. DOI: 10.1111/1462-2920.12527
36. *Mishra J., Singh R., Arora N.K.* Plant growth-promoting microbes: diverse roles in agriculture and environmental sustainability // In: Kumar V., Kumar M., Sharma S., Prasad R., editors. Probiotics and Plant Health. – Springer; 2017. – P. 71–111. DOI: 10.1007/978-981-10-3473-2_4
37. *Mnif I., Ghribi D.* Review lipopeptides biosurfactants: main classes and new insights for industrial, biomedical, and environmental applications // Peptide Sci. – 2015. – 104, № 3. – P. 129–147. DOI: 10.1002/bip.22630
38. *Molina-Santiago C., Pearson J.R., Navarro Y., Berlanga-Clavero M.V., Caraballo-Rodriguez A.M., Petras D., Garcia-Martin M.L., Lamon G., Haberstein B., Cazorla F.M., de Vicente A., Loquet A., Dorrestein P.C., Romero D.* The extracellular matrix protects *Bacillus subtilis* colonies from *Pseudomonas* invasion and modulates plant colonization // Nat Commun. – 2019. – 10, № 1919. doi: 10.1128/spectrum.00939-22

39. *Moreira R.R., De Mio L.L.M.* Potential biological agents isolated from apple fail to control *Glomerella* leaf spot in the field // Biol Control. – 2015. – 87. – P. 56–63. DOI: 10.1016/j.biocontrol.2015.04.020
40. *Myresiotis C.K., Vryzas Z., Papadopoulou-Mourkidou E.* Effect of specific plant-growth-promoting rhizobacteria (PGPR) on growth and uptake of neonicotinoid insecticide thiamethoxam in corn (*Zea mays* L.) seedlings // Pest Manag Sci. – 2015. – 71, № 9. – P. 1258–1266. DOI: 10.1002/ps.3919
41. *Oliveira N.M., Martinez-Garcia E., Xavier J., Durham W.M., Kolter R., Kim W., Foster K.R.* Biofilm formation as a response to ecological competition // PLoS Biol. – 2015. – 13, № 7. – e1002191 https://doi.org/10.1371/journal.pbio.1002232
42. *Omer Bendori S., Pollak S., Hizi D., Eldar A.* The RapP-PhrP quorum-sensing system of *Bacillus subtilis* strain NCIB3610 affects biofilm formation through multiple targets, due to an atypical signal-insensitive allele of RapP // J Bacteriol. – 2015. – 197, № 3. – P. 592–602. DOI: 10.1128/JB.02382-14
43. *Powers M.J., Sanabria-Valentin E., Bowers A.A., Shank E.A.* Inhibition of cell differentiation in *Bacillus subtilis* by *Pseudomonas* protegens // J Bacteriol. – 2015. – 197, № 11. – P. 2129–2138. DOI: 10.1128/JB.02535-14
44. *Qiao J., Yu X., Liang X., Liu Y., Borriss R., Liu Y.* Addition of plant-growth-promoting *Bacillus subtilis* PTS-394 on tomato rhizosphere has no durable impact on composition of root microbiome // BMC Microbiol. – 2017. – 17, № 131. DOI: 10.1186/s12866-017-1039-x
45. *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. DOI: 10.3389/fphys.2017.00667
46. *Rekha K., Kumar R.M., Ilango K., Rex A., Usha B.* Transcriptome profiling of rice roots in early response to *Bacillus subtilis* (RR4) colonization // Botany. – 2018. – 96, № 10. – P. 749–765. DOI: 10.1139/cjb-2018-0052
47. *Saeid A., Prochownik E., Dobrowolska-Iwanek J.* Phosphorus solubilization by *Bacillus* species // Molecules. – 2018. – 23, № 11. – e2879. https://doi.org/10.3390/molecules23112897
48. *Sasse J., Martinoia E., Northen T.* Feed your friends: Do plant exudates shape the root microbiome? // Trends Plant Sci. – 2018. – 23, № 1. – P. 25–41. DOI: 10.1016/j.tplants.2017.09.003
49. *Sen S., Borah S.N., Bora A., Deka S.* Production, characterization, and antifungal activity of a biosurfactant produced by *Rhodotorula babjevae* YS3 // Microb Cell Factories. – 2017. – 16, № 95. DOI: 10.1186/s12934-017-0711-z
50. *Sgroy V., Cassán F., Masciarelli O., Del Papa M.F., Lagares A., Luna V.* Isolation and characterization of endophytic plant growth-promoting (PGPB) or stress homeostasis-regulating (PSHB) bacteria associated to the halophyte *Prosopis strombulifera* // Appl Microbiol Biotechnol. – 2009. – 85, № 2. – P. 371–381. DOI: 10.1007/s00253-009-2116-3
51. *Sivasakthi S., Usharani G., Saranraj P.* Biocontrol potentiality of plant growth promoting bacteria (PGPR) – *Pseudomonas fluorescens* and *Bacillus*

subtilis: A review // Afr. J. Agric. Res. – 2014. – 9, № 12. – P. 1265–1277. https://doi.org/10.5897/AJAR2013.7914

52. *Sorty A.M., Meena K.K., Choudhary K., Bitla U.M., Minhas P., Krishnani K.* Effect of plant growth promoting bacteria associated with halophytic weed (*Psoralea corylifolia* L) on germination and seedling growth of wheat under saline conditions // Appl. Biochem. Biotechnol. – 2016. – 180, № 5. – P. 872–882. DOI: 10.1007/s12010-016-2139-z
53. *Stefanic P., Kraigher B., Lyons N.A., Kolter R., Mandic-Mulec I.* Kin discrimination between sympatric *Bacillus subtilis* isolates // Proc. Natl. Acad. Sci. U.S.A. – 2015. – 112, № 14. – P. 14042–14047. DOI: 10.1073/pnas.1512671112
54. *Tao C., Li R., Xiong W., Shen Z., Liu S., Wang B., Ruan Y., Geisen S., Shen Q., Kowalchuk G.A.* Bio-organic fertilizers stimulate indigenous soil *Pseudomonas* populations to enhance plant disease suppression // Microbiome. – 2020. – 8, № 137. DOI: 10.1186/s40168-020-00892-z
55. *Thérien M., Kiesewalter H.T., Auria E., Charron-Lamoureux V., Wibowo M., Maróti G., Kovács A.T., Beauregard P.B.* Surfactin production is not essential for pellicle and root-associated biofilm development of *Bacillus subtilis* // Biofilm. – 2020. – 2. – e100021. https://doi.org/10.1016/j.bioflm.2020.100021
56. *Townsley L., Yannarell S.M., Huynh T.N., Woodward J.J., Shank E.A.* Cyclic di-AMP acts as an extracellular signal that impacts *Bacillus subtilis* biofilm formation and plant attachment // MBio. – 2018. – 9, № 3. – P. e00341-18. DOI: 10.1128/mBio.00341-18
57. *Trivedi P., Leach J.E., Tringe S.G., Sa T., Singh B.K.* Plant-microbiome interactions: From community assembly to plant health // Nat. Rev. Microbiol. – 2020. – 18, № 10. – P. 607–621. DOI: 10.1038/s41579-020-0412-1
58. *van Gestel J., Vlamakis H., Kolter R.* Division of labor in biofilms: The ecology of cell differentiation // Microbiol. Spectr. – 2015. – 3. – P. 1–24. https://doi.org/10.1128/microbiolspec.mb-0002-2014
59. *Verma P.P., Shelake R.M., Das S., Sharma P., Kim J.Y.* Plant growth-promoting rhizobacteria (PGPR) and fungi (PGPF): Potential biological control agents of diseases and pests // Microbial Interventions in Agriculture and Environment. – 2019. – P. 281–311. DOI: 10.1007/978-981-13-8391-5_11
60. *Vlamakis H., Chai Y., Beauregard P., Losick R., Kolter R.* Sticking together: Building a biofilm the *Bacillus subtilis* way // Nat. Rev. Microbiol. – 2013. – 11, № 3. – P. 157–168. DOI: 10.1038/nrmicro2960
61. *Walukiewicz H.E., Tohidifar P., Ordal G.W., Rao C.V.* Interactions among the three adaptation systems of *Bacillus subtilis* chemotaxis as revealed by an in vitro receptor-kinase assay // Mol. Microbiol. – 2014. – 93, № 5. – P. 1104–1118. DOI: 10.1111/mmi.12721
62. *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, № 4. – P. 744–754. https://doi.org/10.1016/j.cjche.2014.05.020
63. *Wang X., Zhao D., Shen L., Jing C., Zhang C.* Application and mechanisms of *Bacillus subtilis* in biological control of plant disease // Role of Rhizospheric

Microbes in Soil. – Springer, 2018. – P. 225–250. DOI: 10.1007/978-981-10-8402-7_9

64. *Ward E., Kim E.A., Panushka J., Botelho T., Meyer T., Kearns D.B., Ordal G., Blair D.F.* Organization of the flagellar switch complex of *Bacillus subtilis* // J. Bacteriol. – 2019. – 201, № 1. – P. 1–11. doi: 10.1128/JB.00626-18
65. *Webb B.A., Hildreth S., Helm R.F., Scharf B.E. Sinorhizobium meliloti* chemoreceptor McpU mediates chemotaxis toward host plant exudates through direct proline sensing // Appl. Environ. Microbiol. – 2014. – 80, № 11. – P. 3404–3415. doi: 10.1128/AEM.00115-14
66. *Wei F., Hu X., Xu X.* Dispersal of *Bacillus subtilis* and its effect on strawberry phyllosphere microbiota under open field and protection conditions // Sci. Rep. – 2016. – 6. – P. 22611. DOI: 10.1038/srep22611
67. *Woo O.G., Kim H., Kim J.S., Keum H.L., Lee K.C., Sul W.J., Lee J.H. Bacillus subtilis* strain GOT9 confers enhanced tolerance to drought and salt stresses in *Arabidopsis thaliana* and *Brassica campestris* // Plant Physiol. Biochem. – 2020. – 148. – P. 359–367. DOI: 10.1016/j.plaphy.2020.01.032
68. *Xie S.S., Wu H.J., Zang H.Y., Wu L.M., Zhu Q.Q., Gao X.W.* Plant growth promotion by spermidine-producing *Bacillus subtilis* OKB105 // Mol. Plant-Microbe Interact. – 2014. – 27, № 7. – P. 655–663.
DOI: 10.1094/MPMI-01-14-0010-R
69. *Yang Y.M., Pollard A., Höfler C., Poschet G., Wirtz M., Hell R., Sourjik V.* Relation between chemotaxis and consumption of amino acids in bacteria // Mol. Microbiol. – 2015. – 96, № 6. – P. 1272–1282. DOI: 10.1111/mmi.13006
70. *Yu Y., Yan F., Chen Y., Jin C., Guo J.H., Chai Y.* Poly-γ-glutamic acids contribute to biofilm formation and plant root colonization in selected environmental isolates of *Bacillus subtilis* // Front. Microbiol. – 2016. – 7. – e1811. doi: 10.3389/fmicb.2016.01811
71. *Zhang N., Wang D., Liu Y., Li S., Shen Q., Zhang R.* Effects of different plant root exudates and their organic acid components on chemotaxis, biofilm formation, and colonization by beneficial rhizosphere-associated bacterial strains // Plant Soil. – 2014. – 374, № 1. – P. 689–700.
DOI: 10.1007/s11104-013-1915-6

REFERENCES

1. Adam M, Heuer H, Hallmann J. Bacterial antagonists of fungal pathogens also control root-knot nematodes by induced systemic resistance of tomato plants. PLoS One. 2014;9(2): e90402 https://doi.org/10.1371/journal.pone.0090402
2. Allard-Massicotte R, Tessier L, Lecuyer F, Lakshmanan V, Lucier JF, Garneau D, Caudwell L, Vlamakis H, Bais HP, Beauregard PB. *Bacillus subtilis* early colonization of *Arabidopsis thaliana* roots involves multiple chemotaxis receptors. MBio. 2016;7(6): e01664-16 doi: 10.1128/mBio.01664-16.
3. Arrizubieta M, Simón O, Williams T, Caballero P. Determinant factors in the production of a co-occluded binary mixture of *Helicoverpa armigera* alphabaculovirus (HearNPV) genotypes with desirable insecticidal characteristics. PLoS One. 2016;11(10): e0164486 https://doi.org/10.1371/journal.pone.0164486

4. Bardin M, Ajouz S, Comby M, Lopez-Ferber M, Graillot B, Siegwart M, Nicot PC. Is the efficacy of biological control against plant diseases likely to be more durable than that of chemical pesticides? Front Plant Sci. 2015;6:566. DOI: 10.3389/fpls.2015.00566
5. Beauregard PB, Chai YR, Vlamakis H, Losick R, Kolter R. *Bacillus subtilis* biofilm induction by plant polysaccharides. Proc Natl Acad Sci U S A. 2013;110(17):E1621-E1630 DOI: 10.1073/pnas.121898411
6. Berendsen RL, Pieterse CM, Bakker PA. The rhizosphere microbiome and plant health. Trends Plant Sci. 2012;17(8):478-486. DOI: 10.1016/j.tplants.2012.04.00
7. Blake C, Christensen MN, Kovács ÁT. Molecular aspects of plant growth promotion and protection by *Bacillus subtilis*. Bacterial Interactions and Evolution Group, DTU Bioengineering, Technical University of Denmark, Kgs. Lyngby, Denmark. Mol Plant Microbe Interact. 2021;34(1):15-25. doi: 10.1094/MPMI-08-20-0225-CR.
8. Boguslawski KM, Hill PA, Griffith KL. Novel mechanisms of controlling the activities of the transcription factors Spo0A and ComA by the plasmid-encoded quorum sensing regulators Rap60-Phr60 in *Bacillus subtilis*. Mol Microbiol. 2015;96(2):325-348. DOI: 10.1111/mmi.12939
9. Borriss R. *Bacillus,* a plant-beneficial bacterium. In: Lugtenberg B, editor. Principles of Plant-Microbe Interactions. Springer International Publishing; 2015. p. 379-391. DOI: 10.1007/978-3-319-08574-6
10. Bull MJ, Plummer NT. Part 1: The human gut microbiome in health and disease. Integr Med (Encinitas). 2014;13(6):17-22. https://pubmed.ncbi.nlm.nih.gov/26770121/
11. Carvalho FP. Pesticides, environment, and food safety. Food Energy Secur. 2017;6(2):48-60. DOI: 10.1002/fes3.108
12. Cawoy H, Mariutto M, Henry G, Fisher C, Vasilyeva N, Thonart P, Dommes J, Ongena M. Plant defense stimulation by natural isolates of *Bacillus* depends on efficient surfactin production. Mol Plant Microbe Interact. 2014;27(1):87-100. DOI: 10.1094/MPMI-09-13-0262-R
13. Chen WC, Juang RS, Wei YH. Applications of a lipopeptide biosurfactant, surfactin, produced by microorganisms. Biochem Eng J. 2015;103:158-169. DOI: 10.1016/j.bej.2015.07.009
14. Dragos A, Kiesewalter H, Martin M, Hsu CY, Hartmann R, Wechsler T, Eriksen C, Brix S, Drescher K, Stanley-Wall N, Kummerli R, Kovács ÁT. Division of labor during biofilm matrix production. Curr Biol. 2018;28(12):1903-1913. e5. DOI: 10.1016/j.cub.2018.04.046
15. Deng Y, Chen H, Li C, Xu J, Qi Q, Xu Y, Zhu Y, Zheng J, Peng D, Ruan L, Sun M. Endophyte *Bacillus subtilis* evade plant defense by producing lantibiotic subtilomycin to mask self-produced flagellin. Commun Biol. 2019;2(368). DOI https://doi.org/10.1038/s42003-019-0614-0
16. Egamberdieva D, Wirth S, Behrendt U, Abd_Allah EF, Berg G. Biochar treatment resulted in a combined effect on soybean growth promotion and a shift in plant growth promoting rhizobacteria. Front Microbiol. 2016;7(209). https://doi.org/10.3389/fmicb.2016.00209

17. Fan H, Zhang Z, Li Y, Zhang X, Duan Y, Wang Q. Biocontrol of bacterial fruit blotch by *Bacillus subtilis* 9407 via surfactin-mediated antibacterial activity and colonization. Front Microbiol. 2017;8(1973). https://doi.org/10.3389/fmicb.2017.01973
18. Farace G, Fernandez O, Jacquens L, Coutte F, Krier F, Jacques P, Clément C, Barka EA, Jacquard C, Dorey S. Cyclic lipopeptides from *Bacillus subtilis* activate distinct patterns of defence responses in grapevine. Mol Plant Pathol. 2015;16(2):177-187. doi: 10.1111/mpp.12170
19. Fisher MC, Hawkins NJ, Sanglard D, Gurr SJ. Worldwide emergence of resistance to antifungal drugs challenges human health and food security. Science. 2018;360(6390):739-742. DOI: 10.1126/science.aap7999
20. Fita A, Rodriguez-Burruezo A, Boscaiu M, Prohens J, Vicente O. Breeding and domesticating crops adapted to drought and salinity: A new paradigm for increasing food production. Front Plant Sci. 2018;6(978). https://doi.org/10.3389/fpls.2015.00978
21. Flemming HC, Wingender J, Szewzyk U, Steinberg P, Rice SA, Kjelleberg S. Biofilms: An emergent form of bacterial life. Nat Rev Microbiol. 2016;14(9):563-575. DOI: 10.1038/nrmicro.2016.94
22. Freitas MA, Medeiros FH, Carvalho SP, Guilherme LR, Teixeira WD, Zhang H, Pare PW. Augmenting iron accumulation in cassava by the beneficial soil bacterium *Bacillus subtilis* (GBO3). Front Plant Sci. 2015;6(596). https://doi.org/10.3389/fpls.2015.00596
23. Gadhave KR, Finch P, Gibson TM, Gange AC. Plant growth-promoting *Bacillus* suppress *Brevicoryne brassicae* feld infestation and trigger density-dependent and density-independent natural enemy responses. J Pest Sci. 2016;89(4):985-992. DOI: 10.1007/s10340-015-0721-8
24. 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. DOI: 10.1016/j.biocontrol.2016.03.011
25. García-Gutiérrez MS, Ortega-Álvaro A, Busquets-García A, Pérez-Ortiz JM, Caltana L, Ricatti MJ, Manzanares J. Synaptic plasticity alterations associated with memory impairment induced by deletion of CB2 cannabinoid receptors. Neuropharmacology. 2013;73:388-396. DOI: 10.1016/j.neuropharm.2013.05.034
26. Gouda S, Kerry RG, Das G, Paramithiotis S, Shin HS, Patra JK. Revitalization of plant growth promoting rhizobacteria for sustainable development in agriculture. Microbiol Res. 2018;206:131–140. DOI: 10.1016/j.micres.2017.08.016
27. Großkinsky DK, Tafner R, Moreno MV, Stenglein SA, De Salamone IEG, Nelson LM, Roitsch T. Cytokinin production by *Pseudomonas fluorescens* G20-18 determines biocontrol activity against *Pseudomonas syringae* in *Arabidopsis*. Sci Rep. 2016;6(23310). DOI: 10.1038/srep23310
28. Hashem A, Tabassum B, Abd_Allah EF. *Bacillus subtilis*: A plant-growth promoting rhizobacterium that also impacts biotic stress. Saudi J Biol Sci. 2019;26(6):1291–1297. doi: 10.1016/j.sjbs.2019.05.004.

29. Hiltner L. Über neuere Erfahrungen und Probleme auf dem Gebiet der Bodenbakteriologie und unter besonderer Berücksichtigung der Gründüngung und Brache. Arbeit. Deut. Landw. Ges. Berl. 1904;98:59–78. DOI: 10.12691/aees-1-6-1
30. Kiesewalter HT, Andrade CNL, Wibowo M, Strube ML, Maroti G, Snyder D, Jørgensen TS, Larsen TO, Cooper VS, Weber T, Kovács ÁT. Genomic and chemical diversity of *Bacillus subtilis* secondary metabolites against plant pathogenic fungi. mSystems. 2021. 6(1) doi:10.1101/2020.08.05.238063.
31. Kovács ÁT. *Bacillus subtilis.* Trends Microbiol. 2019;27(9):724–725. DOI: 10.1016/j.tim.2019.03.008
32. Kumar AS, Lakshmanan V, Caplan JL, Powell D, Czymmek KJ, Levia DF, Bais HP. Rhizobacteria *Bacillus subtilis* restricts foliar pathogen entry through stomata. Plant J. 2012;72:694–706. DOI: 10.1111/j.1365-313X.2012.05116.x
33. Luo C, Zhou H, Zou J, Wang X, Zhang R, Xiang Y, Chen Z. Bacillomycin L and surfactin contribute synergistically to the phenotypic features of *Bacillus subtilis* 916 and the biocontrol of rice sheath blight induced by *Rhizoctonia solani*. Appl Microbiol Biotechnol. 2015;99:1897–1910. DOI: 10.1007/s00253-014-6195-4
34. Marlow VL, Porter M, Hobley L, Kiley TB, Swedlow JR, Davidson FA, Stanley-Wall NR. Phosphorylated DegU manipulates cell fate differentiation in the *Bacillus subtilis* biofilm. J Bacteriol. 2014;196(1):16–27. DOI: 10.1128/JB.00930-13
35. Mielich-Süss B, Lopez D. Molecular mechanisms involved in *Bacillus subtilis* biofilm formation. Environ Microbiol. 2015;17(3):555–565. DOI: 10.1111/1462-2920.12527
36. Mishra J, Singh R, Arora NK. Plant growth-promoting microbes: diverse roles in agriculture and environmental sustainability. In: Kumar V, Kumar M, Sharma S, Prasad R, editors. Probiotics and Plant Health. Springer; 2017. p. 71–111. DOI: 10.1007/978-981-10-3473-2_4
37. Mnif I, Ghribi D. Review lipopeptides biosurfactants: main classes and new insights for industrial, biomedical, and environmental applications. Peptide Sci. 2015;104(3):129–147. DOI: 10.1002/bip.2263
38. Molina-Santiago C, Pearson JR, Navarro Y, Berlanga-Clavero MV, Caraballo-Rodriguez AM, Petras D, Garcia-Martin ML, Lamon G, Haberstein B, Cazorla FM, de Vicente A, Loquet A, Dorrestein PC, Romero D. The extracellular matrix protects *Bacillus subtilis* colonies from *Pseudomonas* invasion and modulates plant colonization. Nat Commun. 2019;10(1919). doi: 10.1128/spectrum.00939-22
39. Moreira RR, De Mio LLM. Potential biological agents isolated from apple fail to control *Glomerella* leaf spot in the field. Biol Control. 2015;87:56–63. DOI: 10.1016/j.biocontrol.2015.04.020
40. Myresiotis CK, Vryzas Z, Papadopoulou-Mourkidou E. Effect of specific plant-growth-promoting rhizobacteria (PGPR) on growth and uptake of neonicotinoid insecticide thiamethoxam in corn (*Zea mays* L.) seedlings. Pest Manag Sci. 2015;71(9):1258–1266. DOI: 10.1002/ps.3919

41. Oliveira NM, Martinez-Garcia E, Xavier J, Durham WM, Kolter R, Kim W, Foster KR. Biofilm formation as a response to ecological competition. PLoS Biol. 2015;13(7): e1002191 https://doi.org/ 10.1371/journal.pbio.1002232
42. Omer Bendori S, Pollak S, Hizi D, Eldar A. The RapP-PhrP quorum-sensing system of *Bacillus subtilis* strain NCIB3610 affects biofilm formation through multiple targets, due to an atypical signal-insensitive allele of RapP. J Bacteriol. 2015;197(3):592–602. DOI: 10.1128/JB.02382-14
43. Powers MJ, Sanabria-Valentin E, Bowers AA, Shank EA. Inhibition of cell differentiation in *Bacillus subtilis* by *Pseudomonas protegens*. J Bacteriol. 2015;197(11):2129–2138. DOI: 10.1128/JB.02535-14
44. Qiao J, Yu X, Liang X, Liu Y, Borriss R, Liu Y. Addition of plant-growth-promoting *Bacillus subtilis* PTS-394 on tomato rhizosphere has no durable impact on composition of root microbiome. BMC Microbiol. 2017;17(131). DOI: 10.1186/s12866-017-1039-x
45. Radhakrishnan R, Hashem A, Abd_Allah EF. *Bacillus*: a biological tool for crop improvement through bio-molecular changes in adverse environments. Front Physiol. 2017;8(667). DOI: 10.3389/fphys.2017.00667
46. Rekha K, Kumar RM, Ilango K, Rex A, Usha B. Transcriptome profiling of rice roots in early response to *Bacillus subtilis* (RR4) colonization. Botany. 2018;96(10):749–765. DOI: 10.1139/cjb-2018-0052
47. Saeid A, Prochownik E, Dobrowolska-Iwanek J. Phosphorus solubilization by *Bacillus* species. Molecules. 2018;23(11):e2897. https://doi.org/10.3390/molecules23112897
48. Sasse J, Martinoia E, Northen T. Feed your friends: Do plant exudates shape the root microbiome? Trends Plant Sci. 2018;23(1):25–41. DOI: 10.1016/j.tplants.2017.09.003
49. Sen S, Borah SN, Bora A, Deka S. Production, characterization, and antifungal activity of a biosurfactant produced by *Rhodotorula babjevae* YS3. Microb Cell Factories. 2017;16(95). DOI: 10.1186/s12934-017-0711-z
50. Sgroy V, Cassán F, Masciarelli O, Del Papa MF, Lagares A, Luna V. Isolation and characterization of endophytic plant growth-promoting (PGPB) or stress homeostasis-regulating (PSHB) bacteria associated to the halophyte *Prosopis strombulifera*. Appl Microbiol Biotechnol. 2009;85(2):371–381. DOI: 10.1007/s00253-009-2116-3
51. Sivasakthi S, Usharani G, Saranraj P. Biocontrol potentiality of plant growth promoting bacteria (PGPR)-*Pseudomonas fluorescens* and *Bacillus subtilis*: A review. Afr. J. Agric. Res. 2014; 9: 1265-1277. https://doi.org/10.5897/AJAR2013.7914
52. Sorty AM, Meena KK, Choudhary K, Bitla UM, Minhas P, Krishnani K. Effect of plant growth promoting bacteria associated with halophytic weed (*Psoralea corylifolia L*) on germination and seedling growth of wheat under saline conditions. Appl. Biochem. Biotechnol. 2016; 180 (5), 872–882. DOI: 10.1007/s12010-016-2139-z
53. Stefanic P, Kraigher B, Lyons NA, Kolter R, Mandic-Mulec I. Kin discrimination between sympatric *Bacillus subtilis* isolates. Proc. Natl. Acad. Sci. U.S.A. 2015; 112:14042-14047. DOI: 10.1073/pnas.1512671112

54. Tao C, Li R, Xiong W, Shen Z, Liu S, Wang B, Ruan Y, Geisen S, Shen Q, Kowalchuk GA. Bio-organic fertilizers stimulate indigenous soil *Pseudomonas* populations to enhance plant disease suppression. Microbiome. 2020; 8(137). DOI: 10.1186/s40168-020-00892-z
55. Thérien M, Kiesewalter HT, Auria E, Charron-Lamoureux V, Wibowo M, Maróti G, Kovács AT, Beauregard PB. Surfactin production is not essential for pellicle and root-associated biofilm development of *Bacillus subtilis*. Biofilm. 2020; 2:e100021. https://doi.org/10.1016/j.bioflm.2020.100021
56. Townsley L, Yannarell SM, Huynh TN, Woodward JJ, Shank EA. Cyclic di-AMP acts as an extracellular signal that impacts *Bacillus subtilis* biofilm formation and plant attachment. MBio. 2018; 9: e00341-18. DOI: 10.1128/mBio.00341-18
57. Trivedi P, Leach JE, Tringe SG, Sa T, Singh BK. Plant- microbiome interactions: From community assembly to plant health. Nat. Rev. Microbiol. 2020; 18:607-621. DOI: 10.1038/s41579-020-0412-1
58. van Gestel J, Vlamakis H, Kolter R. Division of labor in biofilms: The ecology of cell differentiation. Microbiol. Spectr. 2015; 3. https://doi.org/10.1128/microbiolspec.mb-0002-201
59. Verma PP, Shelake RM, Das S, Sharma P, Kim JY. Plant growth-promoting rhizobacteria (PGPR) and fungi (PGPF): potential biological control agents of diseases and pests. Microbial Interventions in Agriculture and Environment. Springer, Singapore. 2019, 281-311. DOI: 10.1007/978-981-13-8391-5_11
60. Vlamakis H, Chai Y, Beauregard P, Losick R, Kolter R. Sticking together: Building a biofilm the *Bacillus subtilis* way. Nat. Rev. Microbiol. 2013; 11:157-168. DOI: 10.1038/nrmicro2960
61. Walukiewicz HE, Tohidifar P, Ordal GW, Rao CV. Interactions among the three adaptation systems of *Bacillus subtilis* chemotaxis as revealed by an in vitro receptor-kinase assay. Mol. Microbiol. 2014; 93:1104-1118. DOI: 10.1111/mmi.12721
62. 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 (4), 744–754. https://doi.org/10.1016/j.cjche.2014.05.020
63. Wang X, Zhao D, Shen L, Jing C, Zhang C. Application and ьechanisms of *Bacillus subtilis* in biological control of plant disease. Role of Rhizospheric Microbes in Soil. Springer. 2018; pp. 225–250. DOI: 10.1007/978-981-10-8402-7_9
64. Ward E, Kim EA, Panushka J, Botelho T, Meyer T, Kearns DB, Ordal G, Blair DF. Organization of the flagellar switch complex of *Bacillus subtilis*. J. Bacteriol. 2019; 201 doi: 10.1128/JB.00626-18
65. Webb BA, Hildreth S, Helm RF, Scharf BE. *Sinorhizobium meliloti* chemoreceptor McpU mediates chemotaxis toward host plant exudates through direct proline sensing. Appl. Environ. Microbiol. 2014; 80 (11), 3404–3415. doi: 10.1128/AEM.00115-14
66. Wei F, Hu X, Xu X. Dispersal of *Bacillus subtilis* and its effect on strawberry phyllosphere microbiota under open field and protection conditions. Sci. Rep. 2016; 6:22611. DOI: 10.1038/srep22611

67. Woo OG, Kim H, Kim JS, Keum HL, Lee KC, Sul WJ, Lee JH. *Bacillus subtilis* strain GOT9 confers enhanced tolerance to drought and salt stresses in *Arabidopsis thaliana* and *Brassica campestris*. Plant Physiol. Biochem. 2020; 148:359-367. DOI: 10.1016/j.plaphy.2020.01.03
68. Xie SS, Wu HJ, Zang HY, Wu LM, Zhu QQ, Gao XW. Plant growth promotion by spermidine-producing *Bacillus subtilis* OKB105. Mol. Plant-Microbe Interact. 2014; 27:655-663. DOI: 10.1094/MPMI-01-14-0010-R
69. Yang YM, Pollard A, Höfler C, Poschet G, Wirtz M, Hell R, Sourjik V. Relation between chemotaxis and consumption of amino acids in bacteria. Mol. Microbiol. 2015; 96 (6), 1272–1282. DOI: 10.1111/mmi.13006
70. Yu Y, Yan F, Chen Y, Jin C, Guo J.H, Chai Y. Poly-g-glutamic acids contribute to biofilm formation and plant root colonization in selected environmental isolates of *Bacillus subtilis*. Front. Microbiol. 2016; 7:e1811. doi: 10.3389/fmicb.2016.01811
71. Zhang N, Wang D, Liu Y, Li S, Shen Q, Zhang R. Effects of different plant root exudates and their organic acid components on chemotaxis, biofilm formation and colonization by beneficial rhizosphere-associated bacterial strains. Plant Soil. 2014; 374:689-700. DOI: 10.1007/s11104-013-1915-6

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