ADAPTATION AND TOLERANCE OF WHEAT PLANTS TO DROUGHT MEDIATED BY NATURAL GROWTH REGULATORS *Bacillus* spp.: MECHANISMS AND PRACTICAL IMPORTANCE
(review)

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A b s t r a c t

Environmental abiotic factors leading to water deficiency significantly limit the production of major crops worldwide (Z. Ahmad et al., 2018). In the face of rapid population growth and climate change, it is important to ensure food security, which is mainly possible by increasing the productivity of strategically important crops, including wheat, which is used for human consumption in many regions of the world and provides more than 50 % of food energy needs (S. Asseng et al., 2019). Application of beneficial growth-stimulating bacteria *Bacillus* spp. are effective, environmentally friendly and safe natural strategy for protecting plants from stresses resulting in water deficiency (M. Kaushal et al., 2019; A. Hussain et al., 2020; M. Camaille et al., 2021). To date, the growth-stimulating and protective effect of *Bacillus* spp. under various abiotic stresses are indicated for a wide range of plants (S. Moon et al., 2017; H.G. Gowtham et al., 2020; N. Shobana et al., 2020), including wheat (G. Sood et al., 2020; U. Rashid et al., 2021). The mechanisms of this physiological action of *Bacillus* spp. on host plants remain largely unknown. Presumably, it is due to i) competition for space and nutrients with plant pathogens and increased availability of macro- and micronutrients (S. Danish et al., 2019; D. Miljakovic et al., 2020; A. Kumar et al., 2021), ii) production of a wide range of bioactive components and protective compounds (M. Saha et al., 2016; R. Çakmakçi et al., 2017; N. Ilyas et al., 2020), and iii) induction of plant systemic tolerance to stresses (I.A. Abd El-Daim et al., 2019; C. Blake et al., 2021; U. Rashid et al., 2021). The efficacy of the same *Bacillus* strain may vary, depending on many factors including a spectrum of the synthesized compounds, strains, plant species, ecological and geographical origin, varietal characteristics, the types of stresses during the growing season, etc. (A. Khalid et al., 2004; G. Salem et al., 2018; O. Lastochkina et al., 2020). This review summarizes an information on the current state of research and the latest available information on plant-microbe interactions with a focus on protecting wheat against drought. In particular, the mechanisms underlying *Bacillus*-mediated adaptation and tolerance of wheat plants to drought are under consideration. It is shown that *Bacillus* spp. can induce wheat drought tolerance due to i) synthesis of compounds which provide protection against osmotic and oxidative stresses (D. Miljakovic et al., 2020; R. Çakmakçi et al., 2017), ii) intracellular transmission and enhancement of protective signals by a cascade of mediators, iii) regulation of the protective protein gene expression and interorgan transduction with the participation of the main phytohormones, their biosynthesis in the whole plant (U. Rashid et al., 2021), and iv) numerous compounds involved in increasing the bioavailability of macro- and microelements and productivity (A. Hussain et al., 2020; A. Kumar et al., 2021). *Bacillus* spp. can positively influence plant photosynthesis and water exchange (I.A. Abd El-Daim et al., 2019), as well as drought tolerance of wheat genotypes of different agroecological groups (L.I. Pusenkova et al., 2020). The joint use of *Bacillus* bacteria with other natural growth regulators enhance their effectiveness and stability of action (M. Zafar-ul-Hye et al., 2019). The listed commercial bacillary biologicals are effective on wheats. The review contributes to the understanding of the fundamental mechanisms of wheat—*Bacillus* spp. interactions under drought, the development of *Bacillus*-based biologicals and their use in ecologically oriented technologies for wheat growing under changing climate conditions.

Soft wheat (*Triticum aestivum* L.) is the main strategically important cereal crop used for human consumption in many regions of the world and playing a key role in meeting more than 50% of food energy needs [1-4]. Drought, which affects about 64% of the world's agricultural land, is among the dominant abiotic stresses that hinder the growth and loss of yield (up to 50-80%) of wheat [2-5]. Drought, adversely affecting the general metabolism of plants at the physiological, biochemical, and molecular levels, leads to damage to various cellular compartments, degradation of proteins, inactivation of enzymes, decreased absorption of nutrients, transpiration and rate of photosynthesis, closure of stomata, inhibition of growth, wilting and drying of plants [4-6]. Although plants have different defense systems to counter external threats, they are insufficient, due to which significant yield losses are observed for all types of crops, including wheat during drought [4]. According to forecasts, the severity of the drought will consistently increase, which, combined with the exponential growth of the world's population, only exacerbates this problem and requires an urgent solution to prevent an impending food disaster [2, 7]. Plant protection chemicals adversely affect the environment and human health due to high toxicity and the ability to accumulate in products and soils, which, combined with climate change and an increase in the world's population [1, 2], leads to the need to reduce the use of chemicals. This is a serious problem, for the solution of which measures are being taken to increase the stress resistance of plants through genetic modification and traditional breeding [8], which, however, requires a lot of time, significant financial resources and is associated with numerous regulatory restrictions. The use of beneficial microorganisms stimulating plant growth (PGPB, Plant Growth-Promoting Bacteria) [9-12], in particular the genus *Bacillus* spp., capable of activating the natural defense mechanisms of host plants without causing a negative effect on them, the environment and human health, are considered as an affordable, cheap, fast-acting, and environmentally friendly alternative biological strategy for increasing the adaptive potential [13-16] and plant productivity in changing environmental conditions with the simultaneous restoration of soil health [17, 18].

PGPB *Bacillus* spp. is a large and diverse group of useful non-pathogenic microorganisms that live freely in the soil or inhabit the surface (rhizosphere and phylosphere) or the inner part of tissues (endophytes) of host plants, capable of inducing plant growth and resistance to biotic stressors — plant pathogens [19-22], insect pests [20], nematodes [19], viruses [20] and abiotic stresses — drought [17, 24], salinity [11], temperature extremes [12], toxic compounds [14], and UV radiation [12, 13]. This has been demonstrated for many plant species [17, 25-28], including wheat [13, 29-31]. Although the fundamental mechanisms of physiological action of *Bacillus* spp. on plants, to a greater extent remain unclear, it is known that they directly or indirectly interconnected pathways modulate the hormonal background, affecting the architecture of the root system [32-35], improve the bioavailability of macro- and microelements and mineral nutrition of plants (biofixation of nitrogen, solubilization of phosphorus, potassium, zinc and other elements) [36-39], photosynthesis [40, 41], stomatal conductance [17, 42], and water status [17, 42, 43], regulate the production of phytohormones - auxins, cytokinins, gibberellins, abscisic (ABA), salicylic (SA), jasmonic (JA) acids, ethylene, and their accumulation in the plant [23, 44-46], activate the synthesis of various antioxidant and osmoprotective compounds [27, 47, 48],

expression of aquaporin genes sensitive to drought, dehydrins [25, 41], production of volatile organic compounds, exopolysaccharides [49, 50], 1-aminocyclopropane-1-carboxylate deaminase (ACC deaminase) [44, 51-53], organic acids, spectrum of secondary metabolites [41], and signal for shield compounds that activate induced systemic defense in the host plant [25, 35, 42, 52], which leads to an increase in plant resistance and productivity under drought conditions [17]. Along with this, *Bacillus* spp., in particular *B. subtilis*, are generally recognized as safe microorganisms for use in the food industry (GRAS — Generally Recognized As Safe) [12, 13, 16]. In addition, they produce endospores that are extremely tolerant to various physical and chemical influences (heating, drying, organic solvents, UV irradiation, etc.), due to which they retain the ability to trigger defense reactions in host plants even under stressful environmental conditions [19]. All this is done by *Bacillus* spp. attractive agents for the development of commercial biofertilizers and plant protection products on their basis, the number of which is growing every year all over the world. However, in practice, their effectiveness often varies depending on many factors (characteristics of the microorganism strain, the type of plant, its place of growth, varietal characteristics) [13, 34, 54, 55]. For a fuller use of the potential of representatives of *Bacillus* spp. as inoculants that ensure sustainable productivity of crop production (especially against the background of constant climate change), it is extremely important to understand the features of these plant-microbial interactions and the mechanisms underlying the physiological effect that bacilli have on plants, in particular when protecting against dominant environmental stress factors.

The purpose of this review is to summarize the information on the fundamental mechanisms of adaptation and stress resistance caused by the action of *Bacillus* spp., and their role in the practical improvement of growth and maintenance of wheat productivity in drought conditions.

According to current theories, the bacteria *Bacillus* spp. contribute to a more effective resistance of plants to stress due to the development of microbe-induced systemic tolerance (MIST) [27, 42, 52]. It includes a wide range of direct and indirect complex interconnected mechanisms, the action of which causes various morphophysiological and biochemical changes and, reducing the effects of stress on plants, leads to an increase in productivity (see Fig.).

Modification of the root architecture and increasing the availability of elements of mineral nutrition. The main adaptive mechanism of *Bacillus*-mediated stimulation of wheat plant growth under drought conditions is the ability of bacilli, colonizing external (rhizobacteria) and (or) internal (endobacteria) tissues of host plants, to positively modulate plant metabolism and change the architecture of their root system (increase in the length of the main and lateral roots, the density of root hairs, root surface area, and the accumulation of their biomass) [23, 34], which improves the absorption of water and nutrients from the soil [28, 35, 40, 43]. *Bacillus* spp. increase the availability for plants and the assimilation of mineral nutrition elements due to the biofixation of atmospheric N applied with mineral fertilizers, which contributes to a decrease in the doses of fertilizers applied [3, 13, 28, 41]. The participation of *B. subtilis* in the stimulation of the activity of other rhizosphere nitrogen fixers has also been reported [23, 56]. Along with N, plant growth directly depends on P, a large amount of which (more than 80%) is fixed in the soil and is not available for absorption by plants due to adsorption, deposition or transformation. *Bacillus* spp. is able to dissolve water-insoluble and inaccessible to plants forms of soil phosphorus compounds due to the production of organic and inorganic acids,

siderophores, protons, hydroxyl ions and CO_2, which chelate cations or lower the pH to release phosphorus, as well as other biologically active compounds that solubilize P compounds and promoting their assimilation by plants [23, 57, 58]. It was shown that with the presence of N-fixing and P-solubilizing *Bacillus* spp. the absorption of nutrients and the subsequent stimulation of the growth of wheat plants are directly related [23, 58, 59]. Thus, inoculation with *B. subtilis* SIR1 improved the assimilation of NPK by wheat plants at different drought intensities and increased the content of these elements in plants [17]. The study by M. Zafar-ul-Hye et al. [44] showed that *B. amyloliquefaciens* solubilize P, K, which leads to the enrichment of shoots and wheat grains with these elements. In other studies, inoculation of wheat with *B. aryabhattai* strains MDSR7, MDSR11, and MDSR14 significantly increased the availability of Zn for plants, and their growth and accumulation of this element in grains increased [60]. For many *Bacillus* spp. the ability to form biosurfactants positively affecting plant growth was revealed - substances of a lipopeptide nature with surface-active properties capable of reducing the interfacial tension coefficient and emulsifying poorly soluble hydrophobic compounds, increasing their availability for plants [13, 16, 19]. To meet the Fe requirement of *Bacillus* spp. very specific pathways have developed with the participation of low-molecular-weight Fe chelates — siderophores, which, converting Fe into a form accessible to cells, increase its availability for plants and assimilability [38, 61].

Modulation of photosynthesis and water exchange processes. During a drought, the water potential of the soil dramatically decreases, photorespiration increases, stomata close, photosynthesis decreases, cell dehydration and hyperproduction of reactive oxygen species (ROS) occur, which ultimately causes secondary stresses - osmotic and oxidative, leading to inhibition of plant growth and even their death [4, 62] (see Fig.). For many strains of *Bacillus* spp. the ability to maintain the increased relative water content in plants during drought has been shown. This is an important physiological parameter that correlates with drought tolerance [17, 42]. The main physiological criteria for assessing the state of plants during a drought also include stomatal conductance, chlorophyll content, photosynthesis rate, the ratio of variable fluorescence (F_v) and maximum fluorescence (F_m) values, the content of biomarkers of the oxidative and osmotic status of cells, the end product of lipid peroxidation malondialdehyde (MDA) and proline osmolyte, respectively [17]. The positive effects of *Bacillus* spp. have been reported on chlorophyll content, stomatal conductance, and the efficiency of photosystem II in wheat plants during drought [17], primarily due to an improvement in the state of hydration and nutritional profile, which preserve cellular turgor and trigger plant defense mechanisms [42]. It has been shown that the *Bacillus*-mediated improvement of the water status in wheat under stress contributes to an increase in the rate of photosynthesis, since a higher stomatal conductance leads to an increase in CO_2 diffusion in mesophyll cells [40]. Bacterization with the *B. subtilis* strain LDR2 increased the drought tolerance of wheat, maintaining the increased photosynthetic activity of plants, promoting the accumulation of IAA, but reducing the level of ABA and ACC [63]. In the inoculated LDR2 and drought-exposed seedlings, the expression of *TaCTR1* and *TaDREB2* genes, which are responsible for the formation of wheat resistance to abiotic stresses, has increased [63]. According to other data, the manifestation of the protective effect of *B. velezensis* 5113 on wheat during drought was associated with the ability to maintain the photosynthetic apparatus of plants, maintaining a higher content of photosynthetic pigments

[41].
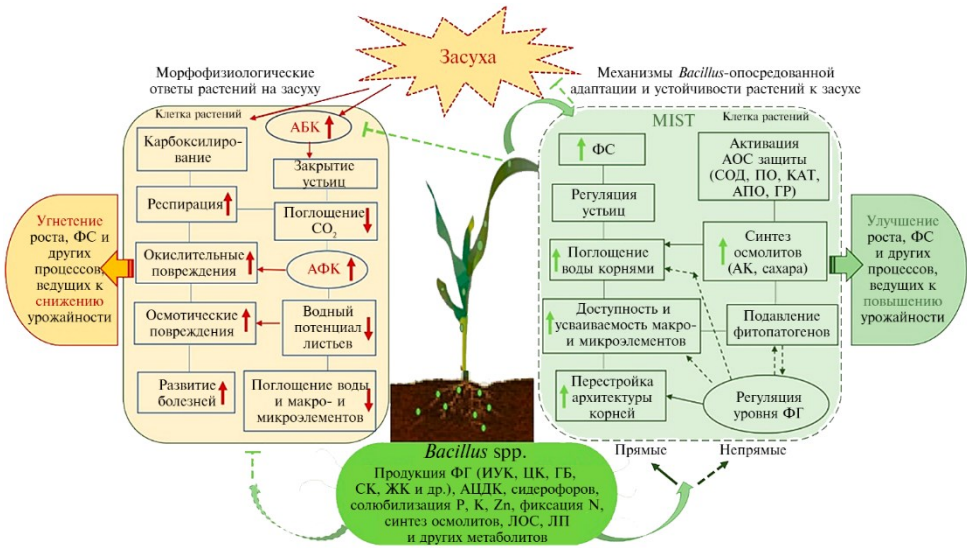
Main mechanisms of *Bacillus*-mediated adaptation and resistance of wheat plants to drought: PH — phytohormones, ABA — abscisic acid, AA — amino acids, AOS — antioxidant system, ROS — reactive oxygen species, ACCD — 1-aminocyclopropane-1-carboxylate deaminase, GB — gibberellins, JA — jasmonic acid, IAA — indolyl-3-acetic acid, VOC — volatile organic compounds, LP — lipopeptides, SA — salicylic acid, SOD — superoxide dismutase, PO — peroxidase, CAT — catalase, APX — ascorbate peroxidase, GR — glutathione reductase, PS — photosynthesis, CK — cytokinins, MIST — microbe-induced systemic tolerance.

A powerful defense *Bacillus*-mediated mechanism of overcoming the osmotic stress and maintaining the water status of plants under drought conditions is the production and accumulation of *Bacillus* spp. a number of polar metabolites, including many amino acids, for example, proline and glycine betaine, and sugars, such as glucose, sucrose, and fructose [26, 35, 41]. Osmolytes produced by *Bacillus* spp. are involved in osmotic regulation of cells and maintain the necessary cellular turgor through a decrease in the water potential of plants without a decrease in their actual water content [13, 26, 35, 42]. The amino acid proline belongs to the main osmolytes that are synthesized and accumulated in plants as a result of protein hydrolysis under the influence of drought. Proline has many functions, including regulating the acidity of the cytosol, minimizing lipid peroxidation by trapping free radicals, and stabilizing subcellular components and structures (proteins and membranes). Involvement of proline in the spectrum of mechanisms of the protective action of *Bacillus* spp. in various species of wild and cultivated plants, including wheat, has been demonstrated in a number of studies [3, 11, 16]. However, the question remains whether the *Bacillus*-mediated increase in proline content in plants is related to its more active absorption from the rhizosphere or to the regulation of biosynthesis in plants [35]. There is evidence on increase in wheat drought resistance under the influence of *Bacillus* spp. with the participation of various other osmolytes [26]. For example, a significant increase in plant drought tolerance was revealed upon inoculation with PGPB strains capable of overproduction of trehalose and / or enhancing its accumulation inside plants [64]. Trehalose is known to play a key role in cell signaling and stabilization of cell structures and proteins [42, 65]. An important place in the maintenance of some strains of *Bacillus* spp. osmotic balance and protection of external proteins in photosystem II during abiotic stress can be occupied by glycine betaine [35]. Thus, the ability of *B. subtilis* GB03 to enhance the biosynthesis of choline (the primary metabolite of glycine betaine biosynthesis) and the accumulation of glycine betaine

in plants was found, which was accompanied by an increase in the relative water content in leaves and the accumulation of dry mass of plants [35, 47]. *B. subtilis*-induced accumulation of glycine betaine (2-fold) and choline (5-fold) imparted drought resistance to *Arabidopsis*, while *B. subtilis*-induced drought resistance was lost in its mutant *xipotl* lines with impaired choline biosynthesis [42, 47]. A number of studies have confirmed the osmoprotective role of sugars in plants inoculated with PGPB during drought [42]. For some strains of *Bacillus* spp. the ability to increase the accumulation of polyamines (cadaverine, spermidine, spermine, and putrescine), the main metabolites that increase the osmotolerance of plants under drought conditions (in addition to the key role of these compounds in cell differentiation, root elongation, and transcriptional regulation), was revealed [35, 66]. Inoculation with *B. megaterium* BOFC15 increased the accumulation of polyamines in plants, which led to polyamine-mediated activation of signaling pathways that mitigated the damaging effect of drought by maintaining an increased amount of water in the plant and photosynthetic activity [66]. The role of cadaverine and spermidine in enhancing root growth in PGPB-treated plants during osmotic stress has been described [23, 35]. For example, an increase in the content of polyamines was observed in *Arabidopsis* plants treated with the spermidine-producing *B. megaterium* BOFC15 strain [66]. The plants were able to survive the drought due to a strong root system with longer primary and lateral roots compared to control samples [66]. Analysis of the filtrate of *B. subtilis* OKB105 culture confirmed that the main growth-stimulating compound was polyamine spermidine, the secretion of which involved the *yecA* and *speB* genes encoding polyamine permease and agmatinase [16]. OKB105-induced expression of expansion genes (*Nt-EXPA1, Nt-EXPA2*) inhibited expression of the ethylene biosynthesis gene *ACO1* [14]. Transcription profiles of *B. subtilis* showed that genes associated with acetylation, transport, and biosynthesis of polyamines are differentially expressed when grown under alkaline or acidic conditions. Literature analysis also indicates the existence of a relationship between polyamines and biofilm formation, which play an important role in the protection of host plants [16], as well as a correlation between the amount of polyamines, ABA, and abiotic stresses [66]. This research area is of interest for uncovering the mechanisms of MIST associated with drought [42]. Recent metabolomic studies have revealed the accumulation of proteins, dehydrins, and a number of other osmoprotective compounds in plants inoculated with bacilli under stress conditions [41]. In particular, the *B. amyloliquefaciens* GB03 strain mitigated osmotic stress by activating drought-sensitive genes for dehydrins and aquaporins, altering hormonal homeostasis, and enhancing the production of antioxidant enzymes and exopolysaccharides [27, 48]. It was reported that exopolysaccharides produced by bacteria are involved in root colonization, improve the water-holding capacity of plants and soil fertility, and also serve to protect the bacterial cells themselves from drying out [50, 67]. In addition, plants inoculated with exopolysaccharide producing PGPB showed higher accumulation of proline, sugars, and amino acids under water stress conditions [50, 67].

Activation of antioxidant defense systems. It is known that drought leads to an imbalance between the formation of ROS (superoxide radical, hydrogen peroxide, and hydroxyl radical) and their neutralization [4, 68]. Excessive amounts of ROS begin to spontaneously and nonspecifically interact with molecular cellular components, which lead to serious disruption of cellular structures, lipids, proteins, carbohydrates, and nucleic acids [62, 68]. The most important mechanisms of *Bacillus*-mediated drought resistance of plants include the participation of these microorganisms in the detoxification of ROS by modulating the natural antioxidant defense systems of plants - as enzymatic (superoxide dismutase, SOD; peroxidase, PO; catalase, CAT; ascorbate peroxidase, APX) and

non-enzymatic (ascorbic acid, AA; glutathione, cysteine, proline, flavonoids, carotenoids, and tocopherol), all of whose components are in complex functional interactions [6, 35] (see Fig.). An increase in the activity of antioxidant enzymes (SOD, PO, CAT) in plants has been reported upon inoculation with *Bacillus* spp. as the main mechanism of MIST protection against drought [13, 17, 35, 42]. Besides, treatment with *B. amyloliquefaciens* 5113 had a protective effect on wheat plants during drought by regulating the activity of the APX *APX1* gene and enzymes of the ascorbate-glutathione complex, which, as is known, due to the high intracellular content of AA and glutathione, provides a high buffer redox capacity of cells and serves as a key player in the antioxidant defense system [68]. Interestingly, under normal conditions, treatment with *B. velezensis* 5113 had practically no effect on the ascorbate - glutathione cycle in wheat, but significantly decreased APX activity under heat stress, while no significant decrease was found under drought and cold stress conditions [41]. Other authors reported that drought increased the activity of stress-related genes *APX1, SAMS1*, and *HSP17.8* in wheat leaves and increased the activity of enzymes of the ascorbate-glutathione cycle, while in plants treated with *B. amyloliquefaciens* 5113, the number of transcripts of these genes decreased, which indicates an improvement in the state of homeostatic mechanisms due to bacterial priming [68]. Obviously, different strains of *Bacillus* spp. can reduce the degree of oxidative damage in different ways with the involvement of various biochemical pathways, which may depend on many factors, including the characteristics of the strain itself, the type of plant, the type of stress, and its intensity. In general, all studies noted an improvement in the state of the entire pro-antioxidant system in plants inoculated with bacilli, which during drought was manifested in a decrease in the content of the end product of lipid peroxidation - MDA [13, 22, 28, 35, 52].

Regulation of phytohormone levels. An important mechanism of *Bacillus*-mediated increase in drought resistance and productivity of plants [16, 23], in particular wheat [13, 68, 70], is the production and (or) regulation of the amount of phytohormones [26, 63, 69, 72] as central connecting links, playing a key role in the reprogramming of ontogenetic and main signaling cascades involved in the formation of plant stress resistance.

It was shown that the filtrates of liquid cultures of *Bacillus* spp. contain phytohormones - auxins, cytokinins, gibberellins, ABA, SA, JA [71, 72], which play an important role in photosynthesis, plant growth, and the integrity of the plasma membrane, as well as in the development of MIST [13, 73-75]. Among the products of *Bacillus* spp. indole compounds, for example, indolyl-3-acetic acid, play a vital role in stimulating plant growth and development, being the main auxin that regulates cell division and elongation, their proliferation and differentiation, the development of vascular tissues, and apical dominance [13, 16]. *Bacillus* spp. use the IAA produced to interact with plants as an element of their colonization strategy, including phytostimulation and bypassing the main defense mechanisms of plants. Numerous studies have shown that IAA-producing bacilli significantly enhance the growth of wheat plants both under normal conditions and during drought [28, 40, 42, 63], causing an increase in the absorption of water and nutrients. An increase in the surface area and length of lateral and adventitious roots due to the high secretion of IAA by bacteria plays a vital role in improving the consumption and assimilation of micro- and macronutrients, in accelerating growth and the formation of drought resistance of plants [13, 42, 70, 76]. According to recent research, *Bacillus* spp. control the level of endogenous IAA in plant roots, regulating the expression of auxin-sensitive genes and thereby causing changes in root architecture

[23]. Drought reduced the IAA content and caused the activation of the *AUX / IAA1* gene in non-inoculated wheat seedlings, while the inoculation with the *B. subtilis* LDR2 strain increased the IAA content (by about 80%), and the *AUX / IAA1* gene expression was suppressed [63]. These data suggest that *B. subtilis* modulates the auxin signaling pathway to protect wheat plants from drought. Biochemical pathways and genes have been identified that control bacterial IAA synthesis; it is assumed that L-tryptophan is the main precursor for IAA formation in microorganisms [77]. However, there may be other pathways for IAA biosynthesis (indole-3-acetamide, indole-3-pyruvate, and tryptamine), and sometimes a bacterial strain possesses more than one pathway for IAA synthesis [77, 78]. It is believed that the ability to produce IAA is most widespread among soil bacteria [75] and is more common among endophytic bacteria than among epiphytic ones [77]. Thus, of the 363 epiphytic and 373 endophytic bacteria studied, the proportion of IAA-producing endophytes was 34%, and of epiphytes, 21% [79]. Another important group of phytohormones produced by *Bacillus* spp. are cytokinins that regulate seed germination, cell division in plant roots and shoots, stomata opening, and nutrient mobilization under drought conditions [23, 28, 31]. It is reported that 90% of P-solubilizing bacteria have the ability to produce cytokinins in vitro [23]. For many strains of *Bacillus* spp. the ability to synthesize gibberellins, which regulate various physiological processes (seed germination, stem elongation, flowering, fruit ripening, as well as leaf and fruit aging), was detected [35, 80]. However, the exact mechanism by which gibberellins promote plant growth during drought is not entirely clear. It is assumed that increased root growth and an increase in root hair density under the influence of gibberellin-producing bacteria are associated with an increased intake of nutrients and water by host plants [69].

Along with an increase in plant drought resistance as a result of microbial colonization, a change in the content of the phytohormone ABA [42], a key participant in the regulation of stress reactions, was recorded [69]. *Bacillus*-mediated shifts in the amount of endogenous ABA led to a change in the architecture of the root system due to an increase in the number of lateral roots and modification of the water status through regulation of the hydraulic conductivity of roots, a decrease in the rate of leaf transpiration, an increase in stomatal conductance, and the induction of the expression of genes involved in ensuring drought resistance [42]. It has been shown that almost 2/3 of 2000 drought-induced genes are regulated by ABA [81]. Treatment with the *B. subtilis* strain LDR2 promoted the maintenance of the photosynthetic activity of wheat plants under drought conditions, while the stress-induced accumulation of ABA and ACC decreased [63]. Since inhibition of ABA biosynthesis suppresses the expression of the aquaporin water transport protein gene *TaAQP7*, the transcriptional activity of which increases under water stress, a decrease in the amount of ABA caused by bacterization of *Bacillus* indicates that bacillus products modulate plant drought resistance through up-regulation of the *TaAQP7* gene. At the same time, seedlings treated with LDR2 were characterized by increased expression of the *TaCTR1* gene, which encodes a key negative regulator of ethylene signal transduction, as well as the gene for the transcription factor *TaDREB2*, which is involved in the regulation of the formation of plant resistance to a wide range of abiotic stresses [63]. According to the authors [63], an increase in wheat drought resistance under the influence of *B. subtilis* LDR2 is due to an increase in IAA and a decrease in ABA: ACC, as well as modulation of the activity of the regulatory component of ethylene signaling CTR1 and the transcription factor DREB2. It has been reported that *B. velezensis* 5113 can use ABA signaling to influence wheat drought tolerance

[41, 43]. In some studies, upon inoculation with bacilli in plants, simultaneously with a decrease in the amount of ABA, the content of SA and JA, which perform signaling functions, had increased [82]. The production of SA and JA by bacteria and (or) the regulation of their exogenous level in plants can play an important role in MIST, since to date there is no doubt about the key role of these phytohormones in triggering a complex chain of defense reactions leading to the formation of plant stress resistance [42, 69]. An increase in the accumulation of endogenous SA in wheat plants in response to inoculation with *B. subtilis* 10-4 correlated with drought resistance of plants, which indicates the involvement of SA-dependent signaling pathways in the implementation of effects mediated by *B. subtilis* [28, 34]. Phytohormones JA and ethylene also play an important regulatory role in the network of interconnected signaling pathways involved in MIST [42, 69]. Although there are reports in the literature on the bacilli-mediated activation of SA-, JA-, and ethylene-dependent signaling pathways involved in the development of a protective response in plants under biotic stresses [83], there is practically no information on the regulation of wheat drought resistance by bacteria with the participation of these signaling pathways. We did not find reports on the role of other phytohormones (for example, brassinosteroids) in microbe-induced systemic drought resistance in wheat plants, although the role of brassinosteroids in mitigating abiotic stresses has been confirmed [69].

Ethylene is another hormone important for plant growth and development, regulating cell growth, seed germination, leaf aging, ripening of flowers and fruits, but the effect of ethylene depends on its concentration in root tissues [69]. During drought, ethylene biosynthesis is enhanced, which negatively affects plant growth and development. ACC deaminase, a key enzyme in the system of ethylene-dependent plant growth regulation, participates in the decomposition reaction of ACC (the direct precursor of ethylene) [52]. Many strains of *Bacillus* spp. were registered as producers of ACC deaminase, and their use showed a decrease in stress-induced accumulation of ethylene, which could otherwise become a growth inhibitor [23, 52]. The use of ACC by bacteria as a source of nutrition leads to a decrease in its content in plants and, as a consequence, to the suppression of ethylene synthesis in the roots. The ethylene precursor ACC is released from the roots into the rhizosphere of the host plant and is cleaved by secreted *Bacillus* spp. ACC deaminase to ammonia and α-ketobutyrate. Ultimately, the ethylene content decrease, which, in turn, promotes plant growth, since with a decrease in ethylene concentration, the absorption of water and nutrients improves [44-46, 50]. The ability of PGPBs producing ACC deaminase, including *Bacillus* spp., to improve wheat growth during drought has been shown [35, 44-46]. For example, under drought conditions in plants inoculated with bacteria *B. amyloliquefaciens* producing ACC deaminase, the intensity of photosynthesis, transpiration, stomatal conductance, the content of chlorophylls a and b, and grain yield increased significantly [44, 46]. According to other studies, inoculation with bacteria producing ACC deaminase led to a noticeable increase in the relative water content in wheat leaves under water stress [54].

The study of the effect of *B. subtilis* LDR2 on the expression of the gene encoding CTR1 (a regulatory component of the ethylene signaling pathway that modulates stress-related changes in plants) showed that, under drought, in LDR2-inoculated wheat seedlings, *TaCTR1* gene expression was higher than in non-inoculated ones, which indicates the involvement of these bacteria in increasing the drought resistance of wheat [63]. Interestingly, although ACC deaminase activity has been described for many *Bacillus* strains, the ACC deaminase genes (structural gene *acdS* and regulatory gene *acdR*) were not identified in 271 strains with a fully sequenced genome [23]. These strains belonged to the

Bacilli class and represented many soil and plant-related species of the genera *Bacillus* and *Paenibacillus* [23].

Biocontrol of phytopathogens and production of metabolites. The indirect mechanisms of *Bacillus*-mediated improvement of wheat plant growth during drought include effective competition and suppression of pathogenic microorganisms (fungi, bacteria) using produced secondary metabolites with antibiotic properties, including ribosomal (bacteriocins) or nonribosomal (lipopeptides, polyketides) peptides with low molecular weight, enzymes that destroy the cell wall of phytopathogens (chitinase, cellulase, glucanase, protease, lipase), siderophores, volatile organic compounds, as well as due to a decrease in the formation of ethylene in plants and activation of MIST against stress [23] (see Fig.). Various *Bacillus* species, including *B. subtilis*, *B. amyloliquefaciens*, *B. cereus*, *B. thuringiensis*, and *B. coagulans*, have been shown to synthesize bacteriocins and bacteriocin-like substances (amylolysin, amizin, subtilin, subtylosin A, subtylosin B, turicin) with antimicrobial properties against phytopathogens. However, bacilli producing nonribosomal lipopeptides and peptides exhibit much stronger antimicrobial properties [23]. Recent studies have shown that lipopeptides also affect the colonization and preservation of *Bacillus* species in the rhizosphere, which stimulates plant defense mechanisms [23]. The most important cyclic lipopeptides produced by bacilli are represented by the surfactin, iturin and fengycin families. It has been shown that *B. subtilis*, *B. amyloliquefaciens*, *B. licheniformis*, *B. pumilus* and *B. coagulans* synthesize lipopeptides of the surfactin family (surfactin, lichenesin, pumilacidin, halobacillin, bamilocin) — heptapeptides that act as antifungal and antibacterial agents. The Iturin family consists of heptapeptides (iturin, mycosubtilin, bacillomycin, bacillopeptins, myxirin, moya-vensin, subtulene produced by *B. subtilis*, *B. amyloliquefaciens*, *B. circans*, *B. pu-milus* and *B. vallismortis*), which have a broad spectrum of fungal inhibiting but less active against bacteria. The production of lipopeptides of the fengycin family (decapeptides fengycin, plipastatin, maltacin), useful for protecting plants from fungal pathogens, was found in *B. subtilis* and *B. amyloliquefaciens* [23]. Non-ribosomal lipopeptides include kurstakins, bacitracins, polymyxins, gramicidins, and thyrokidines. Kurstakins, the cyclic or linear heptapeptides specific for *B. cereus* and *B. thuringiensis* can destabilize the biological membranes of both bacteria and fungi. Bacitracins are cyclic decapeptides produced by *B. licheniformis*, *B. subtilis*, and *B. sonorensis*, whose activity is primarily directed against gram-positive bacteria. Polymyxins are cyclic decapeptides produced by *Paenibacillus polymyxa* that inhibit the growth and reproduction of gram-negative bacteria. Gramicidins and tyrocidins, cyclic decapeptides synthesized by *B. brevis*, are active against a wide range of gram-negative and gram-positive bacteria. Some types of bacilli also produce other nonribosomal peptides (bacilisin, rhizocticin, amicumacin, mycobacillin, and diketopiperazines) and polyketides (bacillin, dihydrobacillin, dificidin, macrolactin) with various antifungal and antibacterial properties. In the most commonly used bioagents *B. subtilis* and *B. amyloliquefaciens*, a significant part of the genetic material (4-5% and 8.5%, respectively) is responsible for the synthesis of secondary metabolites with the potential for the production of more than 20 antimicrobial compounds of different structures. At present, clusters of genes encoding bacteriocins, as well as peptides and polyketides, are easily identified by genomic scanning. For 328 strains of 57 species of the order *Bacillales*, a total of 583 putative clusters of bacteriocin genes were identified; in addition, in 49 species of *Bacillales*, 1231 putative clusters of genes of nonribosomal antimicrobial compounds were found, which were combined into groups according to 23 types of peptides and five types of secondary metabolites of polyketid

nature. [23]. Many studies have shown that hydrolytic enzymes (chitinases, chitosanases, glucanases, cellulases, lipases, and proteases) synthesized by bacilli very actively destroy the cell walls of fungi and bacteria, and also increase plant resistance to stress [13, 23, 84]. The role of siderophores synthesized by bacilli in biocontrol based on competition for Fe in order to reduce its availability for pathogens has been described [23]. Most bacterial siderophores are catecholates, such as bacillibactin produced by some bacilli (eg, *B. subtilis, B. amyloliquefaciens, B. cereus, B. thuringiensis*). In addition, representatives of the genus *Bacillus* produce a wide range of sidero-phores, in particular pyoverdin, pyochelin, schizokinene, petrobactin [23].

Bacillus spp. also secretes extracellular polysaccharides and various volatile organic compounds that change the structure and morphology of roots and cause MIST in plants [85] (see Fig.). Volatile organic compounds are lipophilic in nature and act as signaling molecules for inter- and intraorgan communication and cell-to-cell signaling. Inoculation with *B. amyloliquefaciens* IN937a and *B. subtilis* GB03 induced the production of volatile organic compounds - 2R, 3R-butanediol and 3-hydroxy-2-butanone in *Arabidopsis* plants, which modulated the expression of genes responsible for plant growth. Colonization of *Arabidopsis* roots by the *Pseudomonas chlororaphis* O6 strain induced the production of 2R, 3R-butanediol, which led to stomata closure and increased plant drought resistance; the role of various phytohormones (SA, ethylene, and JA) in the modulation of drought resistance was also established. However, in wheat seedlings treated with *B. thuringiensis* AZP2, an increase in biomass and an increase in plant survival during drought occurred, on the contrary, due to a decrease in emissions of volatile organic compounds, as well as an increase in photosynthesis [35, 40].

The emergence of new research methods allows a broader and more comprehensive assessment of the effect of microbial inoculations on all vital plant systems involved in the regulation of growth and development both under normal conditions and under stress conditions. Thanks to metabolomic studies, it was found that normally inoculated with *B. velezensis* 5113 and non-inoculated wheat plants significantly differed in the accumulation of 61 metabolites: for 36 it increased, for 25 it decreased [41]. In particular, inoculation with *B. velezensis* 5113 increased the content of the amino acids L-proline and L-glutamine, γ-aminobutyric acid (GABA), significantly influenced the metabolism of alanine, aspartate, glutamate and the biosynthesis of flavonoids [41] involved in defense reactions in plants and in interactions between plants and microbes. Drought caused a significant accumulation of metabolites (194 metabolites were found) in the leaves of non-inoculated wheat seedlings compared to control seedlings that were not bacterized and were not subjected to stress. In plants inoculated with *B. velezensis* 5113, drought caused the accumulation of only 139 metabolites. At the same time, under drought conditions, a significant difference between inoculated and non-inoculated wheat plants was noted only for 29 metabolites (the content of 10 increased, 19 decreased) [41]. In particular, treatment with *B. velezensis* 5113 reduced the accumulation of some metabolites associated with the biosynthesis of flavones and flavonols, as well as the intensity of flavonoid biosynthesis in leaves of unstressed and stressed wheat seedlings, which indicates a possible inhibitory effect of *B. velezensis* 5113 on the biosynthesis of flavonoids in plants [41]. The same authors, using proteomic analysis, showed that the treatment of *B. velezensis* 5113 in wheat leaves increased the content of proteins that are involved in the process of photosynthesis [41]. Interestingly, the formation of these proteins

was suppressed in all non-inoculated plants under drought conditions, which indicates an important role of *B. velezensis* 5113 in protecting the photosynthesis process in drought-exposed wheat plants. It was also found that in response to treatment with *B. velezensis* 5113, the synthesis of several proteins with unknown functions is activated in wheat leaves. Of particular note is the fact that wheat plants inoculated with *B. velezensis* 5113 significantly increased the amount of GABA, glutamine, and proline. The role of proline and glutamine in the *Bacillus-mediated* regulation of wheat drought resistance has already been described in the literature [34], but there are no such studies for GABA. There are few data on the participation of GABA in the development of microbial - plant interactions [86]. In particular, it was reported that GABA is synthesized inside legume nodules and is involved in the formation of symbiosis between bacteria and plants. With a moisture deficit under the influence of treatment with the endophytic bacterium *B. subtilis* B26, in the shoots and roots of timothy, the accumulation of GABA increased and the drought resistance of plants increased [87]. The non-protein amino acid GABA, which rapidly accumulates in plant tissues in response to biotic and abiotic stresses, plays a significant role in plant adaptation to stress and is involved in the regulation of physiological and biochemical pathways that ensure plant resistance to stress, including water shortage [78]. GABA is associated with the maintenance of carbon-nitrogen balance, with the metabolism of amino acids, carbohydrates, and growth regulation [86]. In addition, GABA can act as an effective osmolyte with no toxic effects and as an ROS scavenger in plants subjected to abiotic stress. It should be noted that relatively recently, GABA began to be considered as a secondary metabolite and signaling molecule involved in signaling and defense mechanisms in plants [86]. The revealed ability of *B. velezensis* 5113 to modulate the GABA content in unstressed wheat leaves may indicate that this strain is capable of influencing plant resistance to drought through priming, similar to the way it occurs when exogenous GABA is used [41]. Probably, under stress, the accumulation of GABA in plant tissues caused by bacterization contributes to an increase in their resistance, ensuring the formation of a critical link in a cascade of reactions from the perception of a stress signal to sequential physiological responses. This is evidence in favor of the important role of this metabolite in *Bacillus*-mediated drought resistance of wheat, which certainly deserves close attention and further research.

Drought tolerant strains of *Bacillus* spp. and their effectiveness. Particular attention is paid to the isolation of drought-tolerant growth-stimulating strains of *Bacillus* spp. from the rhizosphere of plants living in conditions of moisture deficit, since the growth and survival of bacteria under such conditions determines their ability to mitigate the damaging effect of drought on plants [50, 52]. Recent research by U. Rashid et al. [52] showed that drought-tolerant strains *B. megaterium* MU2 and B. *licheniformis* MU8 from the rhizosphere of plants growing in arid and semi-arid territories cause systemic wheat resistance to drought. In an in vitro experiment, the authors studied 90 isolates of rhizobacteria, of which 38 were found to exhibit one or more PGP properties, including solubilization of P, K and production of exopolysaccharides, but only two strains, *B. megaterium* MU2 and *B. licheniformis* MU8, had the best potential to increase drought resistance of plants (activity of ACC deaminase, IAA production and antagonistic activity against phytopathogens). In addition, when exposed to drought (-0.73 MPa), *B. megaterium* produced three new polypeptides with molecular weights of 18 kDa, 35 kDa, and 30 kDa [52]. Two selected drought-tolerant strains under normal irrigation and drought conditions increased the germination of wheat

seeds by 11-46%, respectively, the viability of seedlings - by 11-151%, the accumulation of wet mass by 35-192%, dry by 58-226%. Moreover, these strains effectively colonized wheat roots and increased the relative water content, the amount of photosynthetic pigments and osmolytes. Thus, after exposure to drought, the survival rate of wheat plants inoculated with *B. megaterium* MU2 increased due to an increase in the relative water content (by 59%), the number of chlorophylls a, b and carotenoids (by 260, 174 and 70%, respectively), protein content (by 136 %), proline (by 117%) and a decrease in MDA formation (by 57%) [52].

Genotypic specificity of the action of *Bacillus* spp. on wheat plants. In practice, the effectiveness of *Bacillus* spp. can vary depending on both environmental conditions and many other factors, including the genotype of plants, their ecological and geographical origin, varietal characteristics, characteristics of strains [34, 54, 55, 88]. The use of representatives of *Bacillus* spp. to increase the yield of field and vegetable crops is limited by the variability of the results obtained in the laboratory, in the greenhouse and in the field [23]. In fact, with repeated introduction (with inoculation of both plants and soil), only 1-2% of PGPB has a positive effect on plant growth comparable to the results of laboratory tests [23]. Analysis of long-term data on the effectiveness of the commercial biological product Fitosporin-M (base *B. subtilis* 26D, Research and Innovation Company BashInkom LLC, Ufa, Russia) in field conditions on spring wheat showed a higher responsiveness to seed treatment with a biological product in arid conditions of the Orenburg and Kurgan regions (increase, respectively, up to 43 and 24%) (55). The specificity of the interaction of Fitosporin-M with different wheat genotypes was revealed, depending on their resistance to drought and belonging to ecotypes. The highest efficiency of Fitosporin-M was noted under arid conditions on spring wheat varieties of the steppe ecotype [55]. The results of laboratory experiments also showed that, under the same growing conditions, wheat varieties belonging to different ecotypes exhibited unequal drought tolerance upon inoculation with *B. subtilis* 26D [88]. The *B. subtilis* strain 26D increased the germination of wheat seeds of the Saratovskaya 55 cultivar (Volga steppe ecotype) during drought, while practically no effect or even inhibited the germination of seeds of the Omskaya 35 cultivar (forest-steppe West Siberian ecotype) [88]. Inoculation with *B. subtilis* 10-4 strain led to similar results, which significantly mitigated the damaging effect of drought on seed germination and plant growth (length of roots and shoots, wet and dry weight) in wheat of the resistant cultivar Ekada 70 (Volga steppe ecotype) on early stages of ontogenesis and did not have a protective effect for the same parameters in relation to the susceptible cultivar Salavat Yulaev (forest-steppe West Siberian ecotype) [34]. Nevertheless, treatment with *B. subtilis* 10-4 induced (albeit to varying degrees) protective responses at the cell level in both varieties, which manifested itself in a decrease in the degree of oxidative and osmotic damage to cells caused by drought and in modulation of photosynthesis and water exchange [34]. Other authors reported that the growth response of wheat to inoculation with bacteria producing ACC deaminase in normal conditions and during drought depended on the plant genotype [46]. It was suggested that such differences are associated either with the composition of root exudates, which is unique for certain wheat genotypes, or with other differences between genotypes that affect their ability to maintain a relatively high number of ACC deaminase producers in the rhizosphere, which requires further study. Identification of features and differences between genotypes and ecotypes of wheat in reactions to inoculation with *Bacillus* spp. could lead to innovative selection strategies to improve plant drought tolerance. Successful use of *Bacillus* spp. in

the field largely depends on the interaction between plants and bacilli, which may be limited by poor colonization of the rhizosphere [23]. The bacillus takes 24 hours to form a biofilm, which promotes root colonization and prolongs the beneficial effects of *Bacillus* strains on the soil. However, colonization of roots with local (aboriginal) bacilli strains is more effective than laboratory or commercial ones. New strategies such as microbiome engineering and selective optimization of microorganisms are helping to detect, modulate and improve target traits, thereby increasing the effectiveness of *Bacillus* spp. and preparations based on them. It is necessary to understand how different strains regulate the growth and development of plants, taking into account the numerous factors affecting the effectiveness of *Bacillus* spp., to clearly determine the characteristics and method of choosing the most effective strains. Transcriptome analysis of the *B. amyloliquefaciens* genome revealed numerous genes involved in ensuring the engraftment of bacteria in the rhizosphere and control of traits useful for plants, including the use of plant polysaccharides, cell motility and chemotaxis, secondary synthesis of antibiotics, and clusters related to plant growth stimulation [23]. It has been shown that root and seed exudates serve as gene inducers, the products of which are involved in root colonization and interactions of plants with bacilli [49, 89, 90]. New studies of the interaction of plants and bacteria are revealing the ability of plants to form their rhizosphere and the microbiome of endoriza [91]. The results obtained to date indicate the existence of other yet unknown mechanisms of Bacillus-mediated drought resistance in wheat, which will be disclosed with the development of technologies for analyzing gene functions [41]. The use of Next Generation Sequencing (NGS) methods in combination with proteomics, metagenomics, and metabolomics will help clarify the details of these interactions, including how this relationship affects plant growth and drought resistance [23, 90].

The use of compositions of *Bacillus* spp. with other bioregulators and microorganisms. In order to improve the effectiveness of *Bacillus* spp. it is of interest to formulate their various combinations with other growth regulators, as well as consortia with other potentially useful microorganisms. For example, bacteria *B. amyloliquefaciens* producing ACC deaminase in combination with organic biofertilization biochar (wood biochar) more effectively mitigated the effect of mild and severe field drought on wheat plants, enhanced their growth and increased productivity compared to the use of *B. amyloliquefaciens* or biochar separately [44]. These results confirmed the data obtained by the authors earlier in laboratory conditions, where the use of B. *amyloliquefaciens* improved the morphological parameters of wheat under conditions of polyethylene glycol-induced drought [45, 46]. In other studies, inoculation with *B. subtilis* 10-4 in combination with SA also more effectively protected wheat plants from drought and the combined effects of drought and fusarium root rot, which manifested itself in a noticeable improvement in growth parameters (length of roots and shoots, accumulation of wet and dry biomass), in modulation of photosynthesis processes, water exchange, and a decrease in the degree of oxidative and osmotic damage [22]. A similar positive effect of the PGPB + SA combination on wheat plants with a lack of water was obtained by N. Khan and A. Bano [50]. During drought, wheat plants (varieties resistant and susceptible to drought) treated with the composition PGPB (*B. cereus* P2, *Planomicrobium chinense* P1) + SA were characterized by a significant increase in the amount of proteins and sugars in the leaves, the content of chlorophyll and the intensity of its fluorescence, as well as a lower synthesis of stress-induced proline, antioxidant enzymes, and a decrease in lipid peroxidation in comparison with control non-inoculated plants and plants inoculated with

PGPB alone [50]. The use of a combination of strains PGPB *Bacillus* spp. and SA appears to be a promising and environmentally sound strategy to reduce the damaging effects of drought on wheat plants. Several authors have reported on the promise of using PGPB in combination with exopolysaccharides to combat drought stress [67]. A study by Y. Li et al. [92] showed that the addition of a superabsorbent polymer (SAP) to a culture of *Bacillus* sp. L-56SAP significantly increased the survival rate of the inoculant and contributed to mitigating the effects of drought on wheat (improved seed germination and plant growth) and increased soil fertility (urease, sucrose and dehydrogenase activity). In addition, *Bacillus* sp. L-56 + SAP significantly increased the chlorophyll content in wheat plants. Real-time qPCR analysis showed that *Bacillus* sp. L-56 + SAP in wheat plants under drought conditions, the expression levels of genes involved in ROS capture (*TaCAT, CsCAT, TaAPX*, and *CsAPX2*), biosynthesis of ethylene (*TaACO2, CsACO1* and *CsACS1*), SA (*TaPR1-1a* and *CsPR1-1a*), and stress responses (*TaDHN3, TaLEA*, and *CsLEA11*), but transcription of the *TaNAC2D* and *CsNAC35* genes is activated [92]. Some researchers reported the effectiveness of using *B. subtilis* CP4 isolated from soil in combination with arbuscular mycorrhiza fungi to increase the accumulation of N, P, Cu, Fe, and Zn in wheat grain, which led to both the biofortification of grain products and increased growth, an increase in photosynthetic activity, yield and production of metabolites in wheat plants under field conditions [65]. Besides, the postharvest physicochemical analysis of soil samples showed that when *B. subtilis* CP4 and fungi of arbuscular mycorrhiza were introduced, the enzymatic status of the soil (invertase, β-glucosidase, dehydrogenase activity) improved in comparison with untreated plots, while it was the combined use of PGPB and fungi to the greatest extent contributed to an increase in soil fertility [65]. Experiments have been reported to study the effect of consortia of *Bacillus* spp. with other PGPBs on the growth and yield of wheat both in laboratory and in the field [39, 93]. Thus, treatment with tetra-combination *B. megaterium + Arthrobacter chlorophenolicus + Enterobacter* sp. *+ Pseudomonas aeruginosa* significantly increased the height of wheat plants (in the greenhouse and in the field experiment by 24.56 and 47.06%, respectively), grain yield (by 75.80 and 40.09%), and straw (by 76.55 and 42.63%) compared to control. The same four-component and two three-component inoculations - *B. megaterium + A. chlorophenolicus + P. aeruginosa* and *A. chloro-phenolicus + Enterobacter* spp. *+ P. aeruginosa* promoted an increase in the yield and absorption of nutrients by wheat [39]. It was reported that inoculation with the *B. megaterium* M3 strain and a combination of bacteria (*B. megaterium* M3 + *B. subtilis* 05U142 + *A. brasilense* Sp245) created a higher supply of wheat plants with nutrients than the application of mineral fertilizers [93]. Similar comparisons with chemically fertilized soils are given in other works [26, 37, 94]. It should be noted that some PGPBs, when inoculated, are capable of negatively affecting mutualistic associations between plants and native soil microorganisms, and this may be the reason for the lack of a favorable effect in some PGPBs [95]. The structure of the wheat rhizobacterium community is very dynamic and depends on various factors: cultivar, plant age, stage of growth, and distance of soil particles from root hairs, nature of root exudation, soil properties and agricultural practices [26, 90]. In general, the accumulated data indicate that the combinations of *Bacillus* spp. with other natural growth regulators and various microorganisms to enhance the growth-stimulating and anti-stress effects of microbiological preparations on plants and increase soil fertility.

Commercialization of bacillary biologics. Many beneficial strains of *Bacillus* spp. commercially available for use as biofertilizers and plant protection products in the form of finished preparations (see Table).

Examples of commercial biologics based on *Bacillus* spp. to stimulate the growth and protection of plants, including wheat

Basis	Biologic	Producer
B. subtilis 26Д	Fitosporin-M	BashInkom Research and Innovation Company, Russia
B. subtilis GB03	Quantum-400	Ecological Laboratories, Inc., USA
B. subtilis QST713	Serenade	AgraQuest, Inc., USA
B. subtilis улуч. GB03	Alinit, Kodiak	Gustafson, Inc., USA
B. subtilis MBI600	Subtilex	Becker Underwood, Inc., USA
B. subtilis Ч-13	BisolbiSan	All-Russia Research Institute of Agricultural Biotechnology, RAAS, Russia
B. subtilis 63-Z	Invivo, Russia	Invivo, Russia
B. subtilis ИПМ215	Baktofit	Sibbiofarm, Russia
B. subtilis В-10 ВИЗР	Alirin-B	AgroBio Tehnologia, Russia
B. subtilis М-22 ВИЗР	Gamair	AgroBio Tehnologia, Russia
B. subtilis ВКМ-В-2604D,		
B. subtilis ВКМ-В-2605D	Vitaplan	VISR, Russia
B. subtilis	Companion	Growth Products, Ltd., USA
B. subtilis	Cease	BioWorks, Inc., USA
B. subtilis	Pro-Mix	Premier Horticulture, Inc., Canada
B. velezensis ABi19	FZB24	ABiTEP GmbH, Germany
B. subtilis	Bio Safe	Lab. Biocontrole Farroupilha, Brazil
B. subtilis	Ecoshot	Kumiai Chemical Industry, Japan
B. subtilis	Biosubtilin	Biotech International, Ltd., India
B. amyloliquefaciens	BioYield	Gustafson, Inc., USA
B. amyloliquefaciens,	Rhizocell GC	Lallemand Plant Care, France
B. velezensis FZB42	RhizoVital®42	ABiTEP GmbH, Germany
B. velezensis FZB45	RhizoVital®45	ABiTEP GmbH, Germany
B. atrophaeus Abi05	RhizoFert®	ABiTEP GmbH, Germany
B. pumilus	Yield Shield	Bayer CropScience, USA
B. pumilus	Ballad Plus	AgraQuest, Inc., USA
B. pumilus	Sonata	AgraQuest, Inc., USA
B. licheniformis	EcoGuard®	Novozymes A/S, Denmark
B. velezensis	Botrybel	Agricaldes, Spain
B. megaterium	Symbion-P	T. Stanes & Co., Ltd., India
Bacillus sp.	Sublic	ELEP Biotechnologies, Italy
Bacillus spp.	Bacillus SPP	Bio Insumos Nativa, Chile

In the world, there is an annual increase in the number of developments of new commercial preparations containing useful strains of bacilli - *B. subtilis, B. megaterium, B. amyloliquefaciens, B. licheniformis, B. pumilus, B. cereus, B. thuringiensis, B. velezensis* [23]. In many works, attention is paid to individual stages of commercialization: the isolation of bacterial strains with useful properties, screening, fermentation methods, mass production, and determination of the viability of the formulation, toxicology, industrial relations, quality control and the effectiveness of practical application [13]. The success of the commercialization of useful strains is influenced by the market demand and popularization of drugs, their safety, stability, shelf life, low cost and ease of use, and the availability of carrier materials [96]. One of the most important aspects of the development and commercialization of effective biological products based on bacilli is the knowledge of the mechanisms of their interaction with plants in normal conditions and especially under stress. In addition, the result of developments largely depends on the effectiveness of interaction between scientific organizations and industries.

Thus, summarizing the literature data indicates the important role of *Bacillus* spp. in the regulation of growth, development and stress resistance of plants, which undoubtedly expands the significance of the practical use of bacilli for increasing drought resistance and productivity of the most important agricultural crops, including wheat. This is also evidenced by the annual increase in the number of basic research, development and distribution of commercial bacillary biological products. At the same time, the results obtained to date indicate the presence of as yet unrevealed mechanisms of *Bacillus*-mediated drought resistance in wheat. In future studies, it seems important to focus on the metabolic pathways

that provide bacilli-induced systemic plant resistance, on expanding knowledge about the spectrum of metabolites produced by bacilli, signaling molecules (phytohormones, amino acids, etc.) and their contribution to the functioning of vital plant defense systems, and also on the identification of new key components responsible for the regulation of wheat drought resistance by bacteria. For a more complete assessment and use of the potential of bacteria *Bacillus* spp. as inoculants that ensure sustainable wheat productivity, it is necessary to understand how different strains stimulate growth and protect plants from stress, and clearly identify the factors contributing to a more effective practical use of these strains, especially in arid conditions of a changing climate. Special attention should be paid to the study of the specificity of the interaction of bacillary strains with different varieties of wheat and the precise selection of their complementary combinations, taking into account the geographical factors of plant growth (climate, soil). It is also important to identify the most effective combinations of *Bacillus* spp. with other natural growth regulators and microorganisms (multistrain consortia), exhibiting an additive effect in protecting wheat from drought and intended for targeted use in various soil and climatic conditions of crop cultivation. In addition, future research should focus on the development of methods for preserving the ability of bacillary strains and (or) their combinations (consortia) with other growth regulators and microorganisms to influence the growth and drought resistance of wheat plants in the field as effectively as in laboratory tests. In-depth study of the mechanisms of interaction of bacilli with wheat plants during drought is based on the integration of modern approaches (NGS, proteomics, and metagenomics and metabolomics methods) in order to develop promising projects and strategies for the practical application of effective and environmentally friendly microbiological preparations.

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