



Potential Aspects of Plant Growth Promoting Bacteria to Improve Horticultural Crop Production

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ABSTRACT

Beneficial microorganisms which help plants to grow better especially under stress conditions are known as plant growth-promoting bacteria (PGPB). These biotic agents, especially *Bacillus subtilis* have well-known role in plant growth promotion and induction of tolerance to stress in plants. They are deemed to act as bio-active and eco-friendly agents to facilitate plant growth under stressful conditions and even to control postharvest decays. Microbial antagonists, including *B. subtilis*, effectively control postharvest diseases of different fruits, vegetables and flowers, which is manifested in prolonged storage period and shelf/vase life, while preserving qualities and reducing weight losses. In this review paper we highlight the potential benefit of PGPBs especially *B. subtilis*, as important biotic useful agents to help horticultural plant perform better under stressful conditions and to delay senescence and control the postharvest deterioration through activation of different defense mechanisms. We further elaborate the underlying mechanisms that PGPB used to help plants to cope with stressful conditions. Nevertheless, the mechanisms of PGPB especially *B. subtilis* action requires further detailed investigations to fully utilize their potentials in horticulture industry.

Introduction

It is predicted that by 2050 the world's population will reach more than 9.1 billion (FAO, 2015; 2019) and to ensure food security,

food production must be increased by at least 70%, mainly due to major crops (FAO, 2015; 2019; Lastochkina et al., 2019). Crop losses due to biotic (pathogens, insects, nematodes etc.) and abiotic stresses (different factors with moisture deficit being a leading cause) can annually reach up to 50-82% yield loss and pose a serious

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danger to food security (Lastochkina et al., 2019). Traditionally using of chemical plant protection products negatively affects the environment and human health due to high toxicity and the ability to accumulate in products and in soils in quantities exceeding the permissible standards. In addition, under conditions of drought or salinization, the concentration of chemical compounds introduced into the soil increases and becomes an additional stress factor, which inevitably leading to crop losses and the production of unsafe food. These problems in combination

with climate change and population growth as well as the tendency to produce organic products increase the relevance of finding ways to increase the sustainability and productivity of crops while minimizing environmental impact. This can be done by developing eco-friendly and affordable approaches to reduce the negative impact of stresses on plants. Therefore, finding practical solution to increase the yield in the area that are encountered with stress condition can help to improve the food security in order to meet the increasing demand for horticultural products in the near future.

Table 1. Effects of plant growth promoting bacteria (PGPB) on production and quality of some horticultural crops

PGPB	Crop	Improving effect	References
<i>Bacillus subtilis</i> V26	Potato	Significant inhibitory effects on the growth of <i>Rhizoctonia solani</i> in <i>in vitro</i> and <i>in vivo</i> conditions.	(Khedher et al., 2015)
<i>Bacillus licheniformis</i> W10	Nectarine fruit	Controlling brown rot caused by <i>Monilinia fructicola</i> via activation of antioxidant and regulation of ROS levels and defense-related enzymes.	(Ji et al., 2020)
<i>Bacillus subtilis</i>	Lettuce	Reduces toxic effects of high electrical conductivity. Positive effect on the biophysics of the photosynthetic electron transport system, which led to decrease in the damaging effects of salinity stress.	(Seifkhalhor et al., 2018)
<i>Bacillus subtilis</i> Rhizo SF 48	Tomato	Protect tomato plants from oxidative damage caused due to drought stress. Promotion of plant growth.	Gowtham et al., 2020)
<i>Bacillus subtilis</i> strain GOT9	<i>Arabidopsis thaliana</i> and <i>Brassica campestris</i>	Enhanced tolerance against salt and drought stresses. Up-regulate drought-inducible genes in <i>Brassica</i> .	(Woo et al., 2020)
<i>Bacillus spp.</i>	Apple 'Golden Delicious'	Protective activity against gray mold caused by <i>Botrytis mali</i> .	(Jamalizadeh et al., 2009)
<i>Bacillus subtilis</i>	Sweet Basil	Increased tolerance to salinity Seed priming by SP improved photosynthetic electron flows and increased non-photochemical quenching in Cd-exposed maize plants	(Abdel-Rahman et al., 2011)
<i>Bacillus licheniformis</i> (strain SA03)	Chrysanthemum	Alleviated saline-alkaline stress in plants with increased survival rates, photosynthesis and biomass.	(Zhou et al., 2017)
<i>Bacillus subtilis</i> 10-4 and 26D	Stored Potato tubers	Increased ascorbic acid content and decreased pathogen-induced proline accumulation and lipid peroxidation in tubers. Prolong shelf life and preserve fresh appearance.	(Lastochkina et al., 2020)

In the present review paper, we would highlight the potential positive effects and challenges for application of plant growth-promoting bacteria (PGPB) with special focus on the *Bacillus subtilis* on horticultural crop

production and quality (Some examples are provided in Table 1). As example, we previously showed that PGPB and an interaction between plant growth regulators and PGPB are important to determine the quality of horticultural crops.

We showed enhancement of the growth-promoting effect of endophytic *B. subtilis* 10-4 both individually and in mixes with salicylic acid (SA) in vegetation phase of plant (Lastochkina et al., 2015), which led to an additional reduction in the incidence of postharvest diseases on stored potato tubers with an extension of their shelf life and preservation of the biological value of the products (Lastochkina et al., 2020; 2020a). Also, we revealed that application of commercial *Bacillus*-based biologicals (Fitosporin-M, Vitaplan) and *B. subtilis* 10-4 significantly reduced *Alternaria alternata*-caused disease development in sugar beet plants and positively influenced growth and roots formation (Lastochkina et al., 2018). Growing interests across the world are directed to understanding PGPB effects, in particular, endophytic *B. subtilis*, which harbor many biotechnological opportunities (Chebotar et al., 2009; 2015). Despite, numerous studies devoted to identification of the mechanisms of PGPB actions, information on the effect of endophytic PGPB on the physiology and mechanisms of inducing plant resistance to stress condition is still demanding. There is also no information on the similarities and differences on the effects of endophytic PGPB isolated from different soil-geographical regions on the stress tolerance of horticultural plants cultivated in different ecological and geographical regions of the world.

Plant growth-promoting bacteria (PGPB)

Beneficial bacteria that stimulate plant growth (PGPB - plant growth-promoting bacteria) activating various physiological characteristics of the metabolism of host plants without causing a negative impact on them, the environment, and consumer health (Van Loon, 2007; Dimkpa et al., 2009; Baez-Rogelio et al., 2016; Maksimov, Khairullin, 2016; Numan et al., 2018, Seifikalhor et al., 2019). Application of PGPB are considered as a safe and environmentally friendly strategy to increase plant resistance/tolerance and productivity (Cao et al., 2012; Ma, 2017; Lastochkina et al.,

2019). PGPB are a group of beneficial microorganisms that live freely in the soil or inhabit the surface (rhizosphere and phyllosphere) and/or the interior of the tissues (endophytes) of host plants. They are capable of enhancing the growth and inducing systemic resistance of plants to a wide range of pathogens (Yang et al., 2006; Droby, 2006; 2009; 2016; Van Loon, 2007; Alfonzo et al., 2009; Beneduzi et al., 2012; Maksimov et al., 2015; Waewthongrak et al., 2015; Shafi et al., 2017; Lastochkina et al., 2019). Various abiotic stresses such as drought, salinization, heavy metals, temperature changes, etc. causing moisture deficiency in plants (Dimkpa et al., 2009; Aliniaiefard et al., 2010, 2016, 2020; Sayed et al., 2011; Cherif et al., 2015; Baez-Rogelio et al., 2016; Kalhor et al., 2018; Lastochkina et al., 2017, 2019, 2020; Numan et al., 2018; Seifikalhor et al., 2018, 2019a,b, 2020). The protective effect of PGPB under water deficit conditions has been shown in a wide range of plants (Asaka and Shoda, 1996; Turan et al., 2012; Rojas-Tapias et al., 2012; Cakmakci et al., 2017; Lastochkina et al., 2017; 2019). Those bacteria which enable to colonize into plant tissues, called endophytes, are usually more successful bacteria than the rhizospheric bacteria in the improvement of plant growth and development under both normal and stress conditions (Pandey et al., 2017; Morelli et al., 2020). The advantage of endophytic bacteria compared to epiphytic bacteria is that, being inside plants, they are less dependent on unfavorable external environmental factors (due to stable pH, humidity, nutrient flow and lack of competition from a large number of microorganisms) and affect the plant metabolism internally (Lastochkina et al., 2019a). In addition, once embedded in plant tissue, endophytic bacteria can contribute to the formation of long-term plant protection against adverse environmental stress factors, both throughout the growing season (thereby contributing to growth and productivity) and

during the post-harvest period during storage (Yang et al., 2006; Sessitsch et al., 2012; Cherif et al., 2015; Pusenkova et al., 2016; Buchholz et al., 2018; Lastochkina et al., 2019; 2019a; 2020; 2020a).

Of particular interest among PGPBs is *Bacillus subtilis*, which is the most attractive and safe (GRAS - Generally Recognized As Safe) agents for use in the food industry and crop production, as natural fertilizers and plant protection products (Pandey et al., 2017; Lastochkina et al., 2017; 2019; Sarma et al., 2018). The beneficial effect of *B. subtilis* in facilitating plant performance under different biotic and abiotic stresses have been shown for various horticultural plant species, including sweet basil (Sayed et al., 2011), cucumber (Egamberdieva et al., 2011), tomato (Asaka and Shoda, 1996; Kilani-Feki et al., 2016), chickpea (Egamberdieva et al., 2017), strawberry (Zhao et al., 2007), melon (Wang et al., 2010; García-Gutiérrez et al., 2013), mango (Govender et al., 2005c), apple (Kim et al., 2015; 2016), kiwi (Kim et al., 2015a), yam (Okigbo, 2005), cabbage (Turan et al., 2014), muskmelons (Yang et al., 2006), artichoke (Saleh et al., 2005), potato (Khedher et al., 2015; Lastochkina et al., 2015; 2020; 2020a), lettuce (Seifikalhor et al., 2018), sugar beet (Pusenkova et al., 2015; Pusenkova et al., 2016; Lastochkina et al., 2018), common bean (Garipova et al., 2020; Gupta and Pandey, 2020) etc.

PGPB roles in plant defense and tolerance responses

To date, there are numerous data indicating the diversity of the physiological effects of PGPB on various plant species (Bochow et al., 2001; Cakmakci et al., 2007; Zhou et al., 2008; 2017; Egamberdieva et al., 2011; 2017; García-Gutiérrez et al., 2013; Verma et al., 2016; Gotor-Vila et al., 2017), which can be divided into pronounced growth-promoting and protective against a wide range of adverse biotic (phytopathogens, pests, nematodes) and

abiotic stress factors (drought, salinization, drops temperatures, UV radiation, high light intensities, etc.) (Sayed et al., 2011; Beneduzi et al., 2012; Turan et al., 2014; Cherif et al., 2015; Pusenkova et al., 2016; Lastochkina et al., 2019; 2020; 2020a). The protective effect of PGPB under water scarcity conditions has been shown for a wide range of horticultural plants, including cucumber, pepper (Chung et al., 2008; Egamberdieva et al., 2011), squash (Turan et al., 2014), tomato (Gupta et al., 2000; Akram et al., 2013), lettuce (Seifikalhor et al., 2018) and some others (Bochow et al., 2001; Zhou et al., 2008; 2017; García-Gutiérrez et al., 2013; Numan et al., 2018; Lastochkina et al., 2019a; Gowtham et al., 2020). The mechanisms by which PGPBs affect a host plant are diverse, intertwined, often specific, and not entirely clear (Niu et al., 2011; Pandey et al., 2017; Lastochkina et al., 2019). According to modern concepts, PGPB, including *B. subtilis*, uses as direct and indirect technique to stimulate growth and induce plant resistance to biotic and abiotic stresses (Dimkpa et al., 2009; Ahmad et al., 2017; Pandey et al., 2017; Numan et al., 2018; Lastochkina et al., 2019; 2019a; 2020; 2020a). Particularly, they influence the synthesis of biologically active compounds, including the production of antibacterial and insecticidal components (Leifert et al., 1995; Mannanov and Sattarova, 2001; Cho et al., 2003; Touré et al., 2004; Romero et al., 2007; Arrebola et al., 2010; Yáñez-Mendizábal et al., 2012; Cawoy et al., 2015; Arroyave-Toroa et al., 2017), biosurfactants (Ongena et al., 2005; 2007; Ongena and Jacques, 2008; Chen et al., 2009; Gong et al., 2013), phytohormones (Turan et al., 2014; Lastochkina et al., 2019) and enzymes (Krebs et al., 1996; Chernin and Chet, 2002; Ahmad et al., 2017; Fan et al., 2017), siderophores and chelators (Ahmad et al., 2017; Pandey et al., 2017). PGPB decrease the level of ethylene, improve nitrogen fixation (Sessitsch et al., 2012), increase the availability of macro- and micro-elements

(Pandey et al., 2017), and incite systemic resistance/tolerance mechanisms (throughout the plant) to biotic and abiotic stresses (Van Loon, 2007; Ongena et al., 2007; Lastochkina et al., 2019).

Numerous studies have shown that PGPBs make an important contribution to reducing the negative effects of water deficiency (Pereyra et al., 2012; Timmusk et al., 2014; Cakmakcı et al., 2017; Barnawal et al., 2017). For example, inoculation with PGPB *Azospirillum brasilense* Sp245 under drought caused a higher level of relative water content and water movement along the apoplast in comparison with uninoculated and stressed plants (Cakmakcı et al., 2017). *A. brasilense* Sp245 increased the size of xylem vessels under conditions of osmotic stress, increasing the level of hydraulic conductivity, which generally improve the water status of inoculated plants and improve the water status in comparison with control samples exposed to osmotic stress (Pereyra et al., 2012). The use of bacteria *A. brasilense* INTA Az-39 increased the yield of plants grown in dry areas due to an increase in the growth rate under the influence of these bacteria, by induction of biomass accumulation (Díaz-Zorita and Fernández-Canigia, 2009).

The revealed ability of PGPB, including *B. subtilis* to launch both systemic acquired resistance (SAR) and system induced resistance (ISR) of plants (Van Loon, 2007) indicates the promise of work on the creation of *B. subtilis*, especially endophytic, biological products to protect plants from different stresses (Pandey et al., 2017; Lastochkina et al., 2019b; 2020b). At the same time, it remains unclear exactly how PGPB, i.e. *B. subtilis* regulates the host plant defense system under stress conditions and as a bacterial defense system of plants interacts with classical signaling pathways. It is believed that the effect of *B. subtilis* is similar to the effect of “weak” pathogens on plants, and on the other hand, they themselves produce metabolites with hormonal and signaling functions (auxins,

cytokinins, ethylene, gibberellins, ABA, SA, jasmonic acid) (Lastochkina et al., 2019; 2019a). In addition, the key targets that *B. subtilis* acts on can be both the signaling pathways of the plants and the whole spectrum of compounds involved in the regulation of the development of a protective response to stresses (García-Gutiérrez et al., 2013; Lastochkina et al., 2019; 2019a).

The most effective as bioagents for protecting plants and increasing their productivity are endophytic PGPBs living inside plant tissues, which allows them to be less dependent on external environmental factors (compared with rhizospheric and phyllospheric strains). This is due to stable pH, humidity, nutrient flow and lack of competition from a large number of microorganisms (Sessitsch et al., 2012; Maksimov and Khairullin, 2016; Pandey et al., 2017; Lastochkina et al., 2019; 2020).

Endophytes are a class of microorganisms that are extremely diverse, and many of them are localized in the host tissues (bark, flowers, roots, stems, leaves and seeds) (Compant et al., 2010; Vasileva et al., 2019). Almost all plants, including cultivated and wild, herbaceous and woody, as well as sphagnum mosses contain endophytes (Vasileva et al., 2019; Žiarovská et al., 2020). Some scientists believe that most of the endophytic bacteria penetrate into plants through the root system, and then spread throughout the plant with the flow of water and nutrients (Compant et al., 2010), or colonization of the aboveground part of plants can occur by airborne droplets through the stomata and lentils (Coutinho et al., 2015; Santoyo et al., 2016). In some cases, the flowers and fruits of plants were inhabited by unique species of endophytes that are not found in the roots, on the basis of which the assumption was made about the presence of endophytes in almost all plant organs (Compant et al., 2010; Partida-Martinez and Heil, 2011; Pitzschke, 2016). Associations of bacteria with plants could arise and gain a foothold as a result of positive selection in

favor of endophytes (Thrall *et al.*, 2007), which suggests a mutually beneficial cooperation. When studying the functional activity of endophytic strains, it turned out that they have a positive effect on the growth and development of a plant organism, and improve the supply of nutrients. Their presence has a positive effect on resistance to stresses of various natures, and in addition, in the course of long-term coevolution of plants and endophytes. The latter acquired the ability to synthesize chemical compounds originally produced by the host plant (Santoyo *et al.*, 2016). Endophytic bacteria are an important part of various plant functions that determine the productive characteristics of plants, as well as the mechanisms of their response to stress. It should be noted that only recently endophytes have received the attention of the scientific community as they gain knowledge of the useful traits that many of these microorganisms can induce in their owners (Vasileva *et al.*, 2019). They promote plant growth and survival by suppressing pathogens and invertebrate pests, remove soil contaminants, including heavy metals, and increase resistance to extreme temperatures and low water availability. At the same time, endophytes, once embedded in plant tissues, can contribute to the formation of their long-term protection against adverse environmental factors over time (Yang *et al.*, 2006; Sessitsch *et al.*, 2012; Cherif *et al.*, 2015; Pusenkova *et al.*, 2015; 2016; Lastochkina *et al.*, 2019; 2019a; 2020). In addition, PGPB such as *B. subtilis* produce spores that are resistant to physical and chemical agents (heating, organic solvents, and UV radiation), which allows them to survive under adverse environmental conditions and retain the ability to trigger protective responses of host plants (Ongena and Jacques, 2008; Gao *et al.*, 2016). All this, combined with the fact that *B. subtilis* are recognized as GRAS bacteria, makes them the most attractive and promising bioagents for the development of new organic and energy-

saving technologies, including natural fertilizers and plant protection products, to improve growth and productivity under stressful conditions (Knox *et al.*, 2000; Mannanov and Sattarova, 2001; Jiang *et al.*, 2001; Leelasuphakul *et al.*, 2006; 2008; Aouadhi *et al.*, 2016).

One of the main reasons currently holding back the development of products based on endophytic bacteria is a lack of knowledge about underlying mechanisms of interaction between PGPB endophytes and host under stress conditions. Moreover, the effectiveness of the same *B. subtilis* strain vary depending on many factors, including the spectrum of the compounds synthesized by the strains, the type of host plants, their ecological and geographical origin, varietal characteristics, susceptibility or immunity to certain environmental stress factors, as well as the nature of the stresses that plants undergo during the growing season, and many others (Lastochkina *et al.*, 2019).

Mechanisms underlying plant responses to PGPB

The mechanisms of *B. subtilis* action on the host plants are numerous, diverse, and often specific (Gupta *et al.*, 2000; Niu *et al.*, 2011; Ahmad *et al.*, 2017; Pandey *et al.*, 2017; Numan *et al.*, 2018; Lastochkina *et al.*, 2020). The action of *B. subtilis* is usually associated with the synthesis of biologically active substances (such as antibacterial and insecticidal components, siderophores and chelators, hormones and enzymes). They have the ability to reduce the level of ethylene in plants, fix nitrogen, improve availability of macro / microelements (Berg, 2009; Arrebola *et al.*, 2010; Arroyave-Toro *et al.*, 2017; Pandey *et al.*, 2017) and induce mechanisms of systemic resistance without direct killing or inhibition of the invading pathogen (Van Loon, 2007; Niu *et al.*, 2011; Sayed *et al.*, 2011; García-Gutiérrez *et al.*, 2013; Saikia *et al.*, 2018) (Fig. 1).

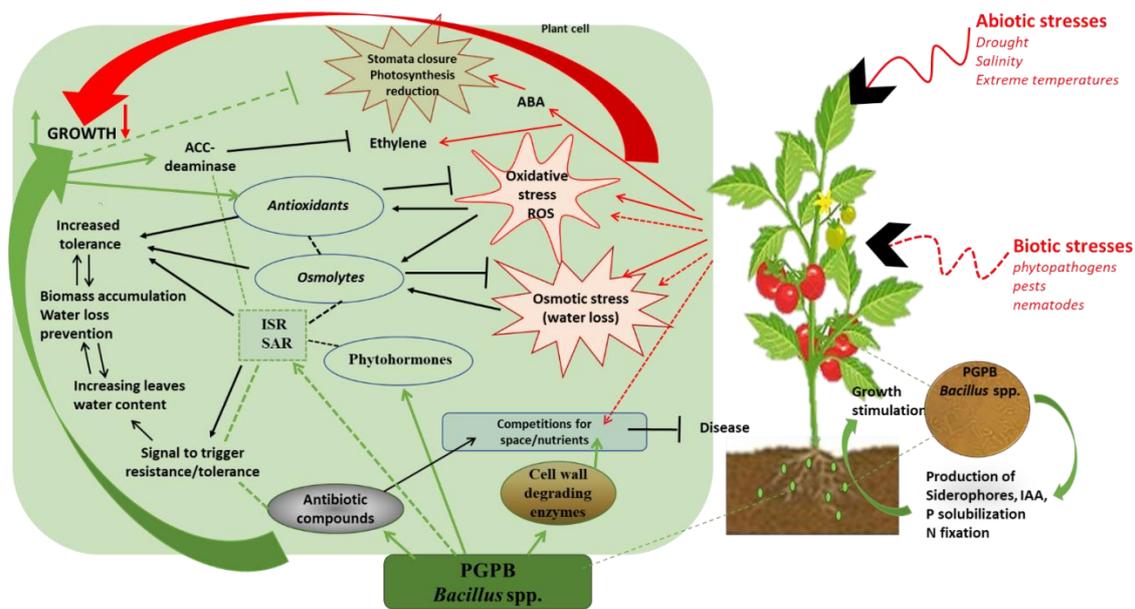


Fig.1. Mechanisms underlying plant growth promoting bacteria-induced plant growth and resistance under biotic and abiotic stresses. ACC-deaminase - 1-aminocyclopropane-1-carboxylic acid deaminase; ABA – abscisic acid; IAA - indole-3-acetic acid; ISR – induced systemic resistance; SAR – systemic acquired resistance; P – phosphate; ROS – reactive oxygen species; N – nitrogen. Green arrows PGPB-induced mechanisms and red arrows stress-induced mechanisms.

Alleviating the damaging effect of abiotic stresses by PGPB leading to the tissue hydrations, and their ability to involve in the regulation of the water status of host plants (Arzanesh et al., 2011). Inoculation of plants with *A. brasilense* and *H. seropedicae* contributed to maintain the relative water content, to conserve the integrity of membrane structures and to increase tolerance to drought (Furlan et al., 2017). It is believed that the implementation of PGPB-induced drought tolerance is based on multiple mechanisms involving antioxidant protection and accumulation of osmolytes (Timmusk et al., 2014; Barnawal et al., 2017), hormonal and ACC-deaminase activity, as well as the induction of systemic (throughout the host plant) resistance (ISR, SAR) (Van Loon, 2007; Saikia et al., 2018; Lastochkina et al., 2019; 2019a) (Fig. 1 and 2).

Drought (both in the above-ground and below-ground) and salinity, as the two main abiotic stresses limiting development of horticultural plant productions (Aliniaiefard and van Meeteren, 2013, 2014, 2016, 2018; Aliniaiefard et al., 2016a,b; Aliniaiefard et al.,

2020; Kalhor et al., 2018; Seifikalhor et al., 2019b; Van meeteren et al., 2020; Shomali and Aliniaiefard, 2020; Fanourakis et al., 2020). Their impacts depend on the growth media and also the stage of plant growth and other factors (Aliniaiefard et al., 2010a,b; 2019; Hassanzadeh et al., 2017). They usually impose oxidative stress in plants resulting from excessive generation of reactive oxygen species (ROS), which are extremely reactive and negatively affect the integrity of the membrane structures of plant cells. An important role in neutralizing the effects of oxidative stress belongs to the antioxidant system (AOS). All of those components are in a complex functional interaction, ensuring plant resistance to stress-induced oxidative damage (Kolupaev et al., 2015). To date, the literature has accumulated evidence on the ability of PGPB to launch an antioxidant plant protection system for host plants by affecting the activity of antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (PO), catalase (CAT) and ascorbate peroxidase (APO), which are involved in the detoxification of ROS (Ullah, Bano, 2015).

Reducing the damaging effect of oxidative stress has been shown in many crops by applying of PGPB (Lastochkina et al., 2017; 2019). Inoculation with a suspension of bacteria *Lactobacillus plantarum* resulted in CAT activation and an increase in the integral antioxidant capacity, down-regulation of oxidative stress caused by dehydration, detected by the accumulation of H₂O₂ and malondialdehyde. With inoculation and co-inoculation with *Bacillus* spp. and *Arthrobacter pascens*, the activity of antioxidant enzymes (including SOD, PO, CAT and APO), as well as the content of sugars and proline increased, which are involved in protecting cells from ROS (Ullah and Bano, 2015). There is evidence of the involvement of *A. brasilense* NO40 and

B. amyloliquefaciens 5113 bacteria, which have protective effects on plants during drought, especially in the regulation of the activity of the ascorbate peroxidase gene APX1 and ascorbate-glutathione complex enzymes (Kasim et al., 2013). PGPBs (*Pseudomonas* sp. E2 and *Azotobacter chroococum* E1) mitigate the adverse effects of drought by maintaining the integrity of the anatomical structures, in particular the thickness of the epidermis, mesophyll and phloem tissues, xylem vessel diameter and size of vascular bundles of the root system, whereas uninoculated samples were characterized by significant anatomical abnormalities under water scarcity conditions (El-Afry et al., 2012).

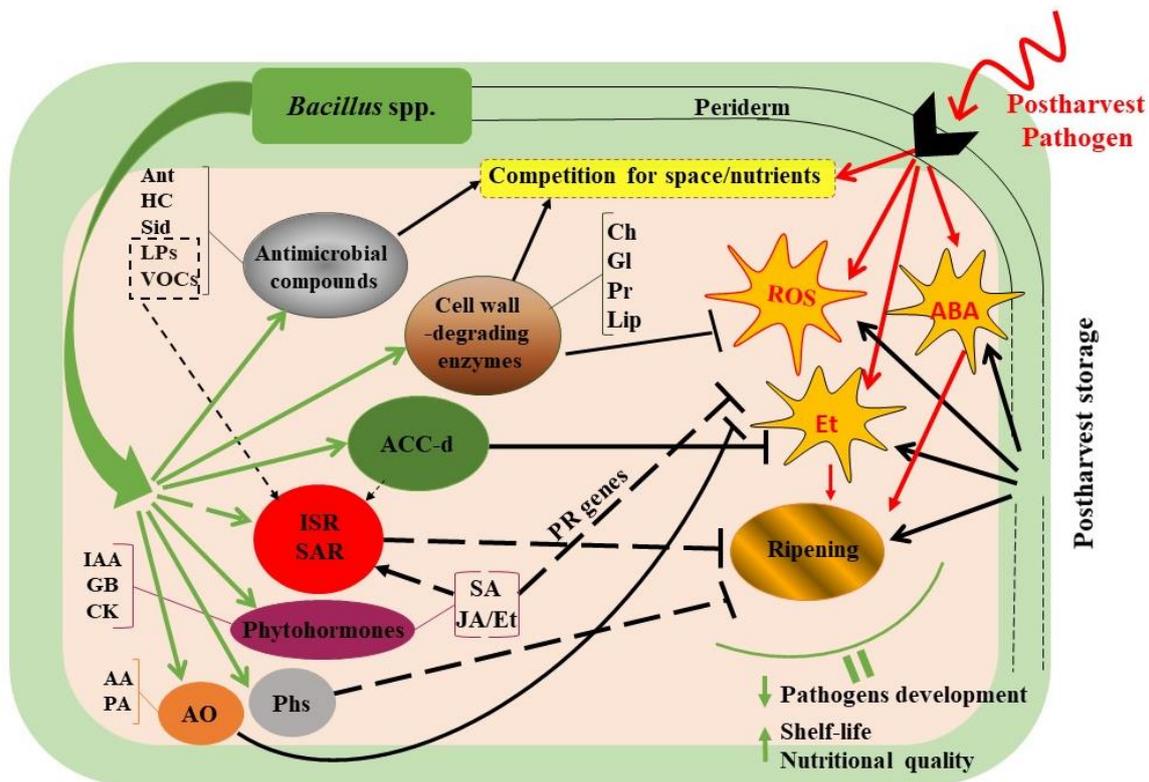


Fig. 2. Mechanisms underlying plant growth promoting bacteria-induced resistance in harvested fruits, vegetables, and flowers in response to biotic stresses. AA - ascorbic acid, ABA - abscisic acid, ACC-d - 1-aminocyclopropane-1-carboxylate deaminase, Ant - antibiotics, AO - antioxidants, Ch - chitinases, CK - cytokinins, Et - ethylene, GB - gibberellins, Gl - glucanases, HC - hydrogen cyanide, IAA - indole-3-acetic acid, ISR - induced systemic resistance, JA - jasmonic acid, Lip - lipases, PA - peroxidase, Pr - proteases, Phs - phytoalexins, ROS - reactive oxygen species, SA - salicylic acid, SAR - systemic acquired resistance, Sid - siderophores (Lastochkina et al., 2019).

A special role in protecting plants from stresses leading to disruption of the water regime is assigned to the key osmoprotectants, proline and dehydrins, which have chaperone properties and are involved in the plant osmoprotection system, reducing the degree of damage to cell structures caused by dehydration (Kolupaev *et al.*, 2015). The involvement of proline in the protective spectrum of PGPB on various species of wild and cultivated plants, has been demonstrated (Dimkpa *et al.*, 2009; Lastochkina *et al.*, 2017). For example, the use of PGPB increased biomass, the relative water content in leaves due to the accumulation of proline in drought-affected maize plants. We previously showed that pre-sowing inoculation with *B. subtilis* 10-4 decreased the level of saline-induced proline accumulation, increased the water-holding capacity of leaves, and increased the linear sizes of seedlings (roots and shoots) and their biomass (Lastochkina *et al.*, 2017). There is evidence of increased stress tolerance under the influence of PGPB, mediated by the accumulation of proline and other various compatible osmolytes (Cakmakci *et al.*, 2017). It has been shown that under water stress, PGPBs are capable of secreting osmolytes, which function in synergy with osmolytes produced by plants and stimulate their growth by regulating the osmotic potential of root cells (Dimkpa *et al.*, 2009). Proteins of dehydrin also act as key osmoprotectants (Allagulova *et al.*, 2003), the intensive synthesis of which observed in plants under the influence of stress factors leading to water stress. The protective functions of dehydrins are due to their structural features, which are manifested in the ability to retain water and prevent the denaturation of cell biopolymers under conditions of dehydration (Allagulova *et al.*, 2003). However, information on the influence of PGPB, including *B. subtilis*, on the level of dehydrins in plants growing under conditions of water deficiency was not found in available literature. Inoculation of rice

plants with a strain *B. amyloliquefaciens* NBRISN13 under salt stress was found to activate the transcription of at least four genes and promoted accumulation of proline and other osmolytes such as betaine and glutamine. These changes are beneficial for effective photosynthesis, growth, and plasma membrane integrity, which eventually improve the plant growth (Nautiyal *et al.*, 2013).

Photosynthesis and water loss through the stomata are the main processes influencing water use efficiency of the crops (Ahmadinik *et al.*, 2020; Alinaieifard *et al.*, 2010, 2020). PGPB may also positively affect the physiological parameters of plants by increasing photosynthetic pigments, total free amino acids, proteins and nitrogen, phosphorous and potassium (NPK) concentrations compared to uninoculated plants under abiotic stresses (Berg *et al.*, 2013). It has been shown that *B. subtilis* induced stomatal closure in a dose- and time-dependent manner when applied to isolated epidermal peels and intact leaves of broad bean. It was revealed that *B. subtilis*-induced stomatal closure in epidermal peels was mediated mainly by ROS production via NADPH oxidases. Furthermore, foliar application of *B. subtilis* significantly reduces stomatal aperture, stomatal conductance, transpiration rate and net photosynthesis rate of leaves of broad bean. As a consequence, the water use efficiency of plants inoculated with *B. subtilis* was higher than that in the control. The chlorophyll fluorescence and content analysis further demonstrated that *B. subtilis* could enhance plant photosynthetic activities by increasing leaf photosynthetic efficiency and chlorophyll content. These results suggest that foliar spray of *B. subtilis* can improve water use efficiency of crops via the regulations of stomatal movement and photosynthetic activity (Li *et al.*, 2016).

PGPB interaction with phytohormones

PGPB are involved in the regulation of signaling pathways of phytohormones such as SA, jasmonic acid (JA), ethylene and others

(Van Loon, 2007; Niu *et al.*, 2011; Sayed *et al.*, 2011; García-Gutiérrez *et al.*, 2013; Saikia *et al.*, 2018). An important role in the manifestation of the anti-stress action of PGPBs is related to their ability to induce the production of endogenous phytohormones, which play a pivotal role in increasing the tolerance of plants to stresses (Lastochkina *et al.*, 2019). The ability of PGPB to synthesize phytohormones such as IAA, ABA, cytokinins, gibberellins, ethylene, SA, JA has been shown in numerous previous studies (Maksimov *et al.*, 2015; Barnawal *et al.*, 2017; Lastochkina *et al.*, 2017; 2019). For instance, inoculation with IAA-synthesizing PGPB stimulated the processes of root formation and growth, which may lead to an increase in the absorption of water and nutrients by these plants under water stress conditions (Dimkpa *et al.*, 2009; Egamberdieva *et al.*, 2017). Inoculation with *A. brasilense* Sp245 contributed to improve the quality of product, the assimilation of mineral nutrition elements (K, Ca, and Mg), maintain the water potential, the absolute and relative water content in tissues, maintain the elasticity of the cell wall, which together have positive effects on development of drought tolerance in many plant species (Creus *et al.*, 2004; Cakmakci *et al.*, 2017). Decrease in the water potential of leaves and a simultaneous increase in their water content is a consequence of the ability of these bacteria to produce IAA, to induce the formation and growth of lateral roots of plants, and thus increase the level of absorption of water and nutrients under drought conditions (Arzanesh *et al.*, 2011). ABA is the main phytohormone that reduces transpiration by provoking stomatal closure under the condition of high evaporative demand. In response to the action of stress factors causing cell dehydration in plants, rapid synthesis and accumulation of ABA is observed (Aliniaiefard, 2014; Aliniaiefard *et al.*, 2014; Aliniaiefard and van Meeteren, 2013, 2014; van Meeteren and Aliniaiefard, 2015). To date, the regulation of the

biosynthesis and accumulation of ABA and the main stages of its signaling in plants under the influence of water stress have been identified. Dehydration directly or indirectly can affect the enzymatic activity of the calcium signaling system associated with membrane-bound phospholipase-C. During the hydrolysis of membrane phospholipids under the action of phospholipase-C, 1,4,5-triphosphates are formed, which cause the opening of calcium channels. An increase in the concentration of calcium in the cytosol leads to an increase in protein kinase activity, which phosphorylates regulatory transcription factors that activate the expression of genes and enzymes involved in ABA biosynthesis. Secondary mediators, such as H₂O₂, may be involved in ABA regulation of transcription of ABA-sensitive genes. The accumulation of peroxide is associated with the ability of ABA to increase the activity of NADPH oxidase, ROS, phospholipids, calcium channels and the formation of nitric oxide (NO) (Aliniaiefard, 2014; Aliniaiefard, van Meeteren, 2013; Shomali and Aliniaiefard, 2020; Van Meeteren *et al.*, 2020). It is known that about 2/3 of the 2000 drought-induced genes are regulated by ABA (Huang *et al.*, 2008), which underlies the adaptation of plants to various stresses leading to disruption of the water regime. It has been found that some PGPB strains increase the levels of ABA secreted by plants when exposed to water stress. However, it is not yet clear whether ABA is synthesized by bacteria or plants. Moreover, it was shown that inhibition of ABA biosynthesis inhibits the expression of TaAQP7 aquaporin gene (encoding a protein of water transport), the activity of which increases when exposed to water stress. These data indicate the involvement of ABA in the up-regulation of the TaAQP7 gene as a modulator of plant drought tolerance. The rhizobacteria *B. subtilis* (LDR2), *Arthrobacter protophormiae* (SA3) and *Dietzia natronolimnaea* (STR1) contributed to the maintenance of photosynthetic activity of plants under

drought conditions, while bacterialization with strains of LDR2 and SA3 reduced the stress-induced accumulation of ABA and ACA bacteria, whereas did not significantly affect their contents (Barnawal et al., 2017). The seedlings pretreated with strains SA3, STR1, and LDR2 were characterized by an increase in the expression activity of the TaCTR1 gene encoding the key negative regulator of ethylene signal transduction, as well as the gene encoding the TaDREB2 transcription factor, which is involved in the regulation of the formation of plant resistance to a wide range of abiotic stress factors. An increase in the resistance of plants to drought and salinization under the influence of inoculation with rhizobacteria *B. subtilis* LDR2, *A. protophormiae* SA3 and *D. natronolimnaea* STR1 is due to a simultaneous increase in IAA and a decrease in ABA and ACC, modulation of the activity of the CTR1-regulatory component of ethylene signaling and DREB2 transcription factor (Barnawal et al., 2017).

Many studies have shown that ABA plays an important role in stomata closure in response to moisture deficiency, contributing to plant survival under extreme conditions (Acharya, Assmann, 2009; Su et al., 2017), although a stomatal closure pathway independent of ABA has been proposed (Roychoudhury et al., 2013). Since stomata are the gateway to gas exchange between the inside of the leaf and the outside atmosphere, for plants, precise regulation of the stomatal opening is critical to balance CO₂ absorption for photosynthesis while preventing excessive transpiration loss of water. Evolution has led to the creation of a complex network of signaling pathways that cause stomata to open or close in response to environmental signals. It can be assumed that one of the mechanisms of the protective action of *B. subtilis* may be their ability to regulate stomata and photosynthesis with the involvement of endogenous ABA. However, in the available literature, detailed information on the effect of

B. subtilis on both stomatal conductivity, photosynthesis, and the level of endogenous stress phytohormone ABA and the expression of genes involved in the formation of plant resistance with the involvement of ABA-dependent under conditions of drought and salinization is practically absent. There is information about the effect of PGPB in regulating the formation of plant resistance in response to pathogenic infections. For example, Wu et al. (2018) showed that colonization of roots with rhizospheric *B. amyloliquefaciens* FZB42 limits pathogen-mediated re-opening of stomata in *N. benthamiana* plants. *B. amyloliquefaciens* FZB42-induced stomata closure of tobacco plants during pathogenic infection was mediated by ABA and SA-regulated pathways. There is evidence showing improvement of plant growth upon their inoculation by *B. thuringiensis* AZP2, which contributed to a significant increase in the survival rate of plants under drought conditions, due to a significant decrease in the level of carbon dioxide released and an increase in the intensity of photosynthesis (Timmusk et al., 2014). Bacteria *Burkholderia phytofirmans* PsJN is able to reduce the damaging effect of drought on plants through improvement of CO₂ assimilation, which led to an increase in photosynthesis, an increase in chlorophyll content and water efficiency compared to uninoculated plants (Naveed et al., 2014).

A significant role in the adaptation of plants to drought can be related to a non-protein amino acid gamma-aminobutyric acid (GABA), which is involved in the regulation of physiological and biochemical pathways of plants to make them resistant to adverse stress conditions. More recently, GABA has begun to be seen as a secondary metabolite and signal molecule involved in plant signaling and defense mechanisms (Seifikalhor et al., 2019b). The role of GABA as a signal in animals was documented more than 60 years ago, however, evidence that GABA is a signal

in plants appeared only in the last two decades, and only a few years ago a mechanism by which this could happen was identified, a plant 'GABA receptor' that inhibits anion passage through the aluminum-activated malate transporter family of proteins (ALMTs) (Ramesh *et al.*, 2016). Rapid accumulation of GABA in stressed tissue is thought to be involved in enhanced resistance by providing a critical link in the chain of events leading from perception of environmental stresses to timely physiological responses. In addition, there is evidence of the involvement of GABA in the formation of microbial-plant interactions (Kalhor *et al.*, 2018; Seifikalhor *et al.*, 2020; Seifikalhor *et al.*, 2019b). For example, it was found that GABA is synthesized inside legume nodules and is involved in the formation of a symbiosis between bacteria and plants (Suliman, Schulze, 2010). It was shown that with moisture deficiency under the influence of treatment with *B. subtilis* B26 endophytic bacterium in the shoots and roots of timothy, the accumulation of GABA increased and the drought tolerance of plants increased (Gagné-Bourque *et al.*, 2016). It is suggested that GABA accumulation could play a role in increasing the resistance of timothy inoculated with *B. subtilis* B26 (Gagné-Bourque *et al.*, 2016). Information on the influence of *B. subtilis* on the accumulation of GABA and drought tolerance of plants is still demanding.

SA-dependent or JA-dependent protective responses are the dominant primary signals of the local and systemic induced protective responses of plants to stresses (Shakirova *et al.*, 2012). Anti-stress effect of bacteria on plants can be attributed to their ability to synthesize anti-stress compounds (Sayed *et al.*, 2011; García-Gutiérrez *et al.*, 2013). There is evidence that the key target that PGPB acts on is the signaling pathways of the plants that regulate the development of a protective response to stress (Niu *et al.*, 2011). For example, *B. subtilis* UMAF6639 formed the

resistance of melon to powdery mildew by activating JA- and SA-dependent defense reactions (García-Gutiérrez *et al.*, 2013). *B. cereus* AR156 induced systemic resistance of Arabidopsis via the NPR-1 and SA-dependent signaling pathways without affecting the JA/ethylene-dependent pathways (Niu *et al.*, 2011). Chickpea resistance by PGPB (*Pseudomonas*) also occurred due to the production of phenolic compounds and the induction of systemic resistance through SA-dependent signaling pathway (Singh *et al.*, 2003). Endophytic bacteria (*Achromobacter xylosoxidans*, *B. pumilus*) enhance the growth of sunflower plants under water stress through the production of endogenous SA (García-Gutiérrez *et al.*, 2013). It was revealed that treatment of *B. amyloliquefaciens* FZB42 in wild-type plants led to overexpression of the PR-1a, LOX, and ERF1 genes involved in SA, JA, and ethylene-dependent signaling pathways (Wu *et al.*, 2018).

In this regard, the use of endophytic *B. subtilis* together with natural and safe signaling molecules with pronounced anti-stress activity is of particular interest. These, in particular, include SA and 24-epibrassinolide (EBR) - recognized inducers of the systemic resistance of plants to diseases and abiotic stresses (Shakirova *et al.*, 2012). To date, a large body of information has been accumulated indicating the participation of SA and EBR in the regulation of protective reactions of various plant species, to water deficiency (Verma *et al.*, 2016).

Conclusion

In conclusion, application of PGPB and compositions of PGPB with other natural growth regulators, including signaling molecules which recognized as the inducers of plant systemic resistance to diseases and abiotic stresses, have a great potential to help horticultural plants to recover from stress conditions and the possibility of the application of these environmentally friendly

biotic agents to improve the quality of horticultural crops.

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References

1. Abdel-Rahman S.S, Abdel-Kader A.A, Khalil S.E. 2011. Response of three sweet basil cultivars to inoculation with *Bacillus subtilis* and arbuscular mycorrhizal fungi under salt stress conditions. *Nature and Science* 9, 93-111.
2. Ahmadinik A, Rahimikhoob A, Aliniaiefard S. 2020. Water use efficiency in novel integrated system of greenhouse and saltwater evaporative pond. *Desalination* 496, 114698.
3. Aliniaiefard S, Tabatabaei S. 2010. Use of Chlorophyll meter for nitrogen management and recommendation of optimum nitrogen concentration in soilless culture of lily. *Floriculture and Ornamental Biotechnology* 4, 63-67.
4. Aliniaiefard S, Rezaei-Nejad A, Seifi-Kalhor M, Shahlai A, Aliniaiefard A. 2010. Comparison of soil and perlite (with nutrient solution supply) growing media for cultivation of lemon verbena (*Lippia citriodora* var. 'Verbena'). *Medicinal and Aromatic Plant Science and Biotechnology* 4, 30-33.
5. Allagulova C.R, Gimalov F.R, Shakirova F.M, Vachitov V.A. 2003. The plant dehydrins: structure and putative functions. *Biochemistry (Moscow)* 68, 945-951.
6. Aliniaiefard S, van Meeteren U. 2013. Can prolonged exposure to low VPD disturb the ABA signalling in stomatal guard cells? *Journal of Experimental Botany* 64, 3551-3566.
7. Aliniaiefard S. 2014. Signal transduction pathways in guard cells after prolonged exposure to low vapour pressure deficits. PhD thesis, Wageningen University.
8. Aliniaiefard S, Malcolm Matamoros P, van Meeteren U. 2014. Stomatal malfunctioning under low Vapor Pressure Deficit (VPD) conditions: Induced by alterations in stomatal morphology and leaf anatomy or in the ABA signaling? *Physiologia Plantarum* 152, 688-699.
9. Aliniaiefard S, Hajilou J, Tabatabaei S.J. 2016a. Photosynthetic and growth responses of olive to proline and salicylic acid under salinity condition. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* 44, 579-585.
10. Aliniaiefard S, Hajilou J, Tabatabaei S.J, Sifi-Kalhor M. 2016b. Effects of ascorbic acid and reduced glutathione on the alleviation of salinity stress in olive plants. *International Journal of Fruit Science* 16, 395-409.
11. Aliniaiefard S, van Meeteren U. 2016. Stomatal characteristics and desiccation response of leaves of cut chrysanthemum (*Chrysanthemum morifolium*) flowers grown at high air humidity. *Scientia Horticulturae* 205, 84-89.
12. Aliniaiefard S, van Meeteren U. 2018. Natural genetic variation in stomatal response can help to increase acclimation of plants to dried environments, 1190 ed. *Acta Horticulturae* 71-76.
13. Aliniaiefard S, van Meeteren U. 2018. Greenhouse vapour pressure deficit and lighting conditions during growth can influence postharvest quality through the functioning of stomata. *Acta Horticulturae* 1227, 677-684.
14. Aliniaiefard S, Shomali A, Seifikalhor M, Lastochkina O. 2020. Calcium signaling in plants under drought, In: Hasanuzzaman M, Tanveer M. (Eds.), *Salt and drought stress tolerance in plants: Signaling networks and adaptive mechanisms*. Springer International Publishing, Cham 259-298.
15. Alfonzo A, Conigliaro G, Torta L, Burruano S, Moschetti G. 2009. Antagonism of *Bacillus subtilis* strain AG1 against vine wood fungal pathogens. *Phytopathologia Mediterranea* 48, 155-158.
16. Arrebola E, Jacobs R, Korsten L. 2010. Iturin A is the principal inhibitor in the biocontrol activity of *Bacillus amyloliquefaciens* PPCB004 against postharvest fungal pathogens. *Journal Applied Microbiology* 108(2), 386-395.
17. Arroyave-Toroa J.J, Mosquera S, Villegas-Escobar V. 2017. Biocontrol activity of *Bacillus subtilis* EA-CB0015 cells and lipopeptides against postharvest fungal pathogens. *Biological control* 114, 195-200.
18. Arzanesh M.H, Alikhani H.A, Khavazi K, Rahimain H.A, Miransari M. 2011. Wheat (*Triticum aestivum* L.) growth enhancement by *Azospirillum* sp. under drought stress. *World Journal of Microbiology and Biotechnology* 27, 197-205.
19. Asaka O, Shoda M. 1996. Biocontrol of *Rhizoctonia solani* damping-off of tomato with

- Bacillus subtilis* RB14. Applied and Environmental Microbiology 62, 4081-4085.
20. Acharya B.R, Assmann S.M. 2009. Hormone interactions in stomatal function. Plant Molecular Biology 69, 451-462.
 21. Ahmad Z, Wu J, Chen L, Dong W. 2017. Isolated *Bacillus subtilis* strain 330-2 and its antagonistic genes identified by the removing PCR. Scientific Reports 7(1), 1777.
 22. Aouadhi C, Rouissi Z, Kmiha S, Mejri S, Maaroufi A. 2016. Effect of sporulation conditions on the resistance of *Bacillus Sporothermodurans* spores to nisin and heat. Food Microbiology 54, 6-10.
 23. Baez-Rogelio A, Morales-Garcia Y.E, Quintero-Hernandez V, Munoz-Rojas J. 2016. Next generation of microbial inoculants for agriculture and bioremediation. Microbial Biotechnology 10(1), 19-21.
 24. Barnawal D, Bharti N, Pandey S.S, Pandey A, Chanotiya S.C, Kalra A. 2017. Plant growth promoting rhizobacteria enhance wheat salt and drought stress tolerance by altering endogenous phytohormone levels and TaCTR1/TaDREB2 expression. Physiologia Plantarum 161(4), 502-514.
 25. Berg G. 2009. Plant-microbe interactions promoting plant growth and health: perspectives for controlled use of microorganisms in agriculture. Applied Microbiology and Biotechnology 84(1), 11-18.
 26. Berg G, Alavi M, Schmidt C.S, Zachow C, Egamberdieva D, Kamilova F, Lugtenberg B. 2013. Biocontrol and osmoprotection for plants under saline conditions. In: Molecular microbial ecology of the rhizosphere, (Ed.: Frans J. de Bruijn). Wiley-Blackwell, USA.
 27. Beneduzi A, Ambrosini A, Passaglia L. 2012. Plant growth-promoting rhizobacteria (PGPR): their potential as antagonists and biocontrol agents. Genetic and Molecular Biology 35(4), 1044-1051.
 28. Bochow H, El-Sayed S.F, Junge H, Stavropoulou A, Schmiedeknecht G. 2001. Use of *Bacillus subtilis* as biocontrol agent. IV. Salt-stress tolerance induction by *Bacillus subtilis* FZB24 seed treatment in tropical vegetable field crops, and its mode of action. Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz 108(1), 21-30.
 29. Buchholz F, Kostic T, Sessitsch A, Mitter B. 2018. The potential of plant microbiota in reducing postharvest food loss. Microbial Biotechnology 11(6), 971-5.
 30. Cakmakci R, Donmez M.F, Erdogan U. 2007. The effect of plant growth promoting rhizobacteria on barley seedling growth, nutrient uptake, some soil properties, and bacterial counts. Turkish Journal of Agriculture and Forestry 31, 189-199.
 31. Cao Q, Den Camp R.O, Kalhor, M.S, Bisseling T, Geurts R. 2012. Efficiency of *Agrobacterium rhizogenes*-mediated root transformation of *Parasponia* and *Trema* is temperature dependent. Plant Growth Regulation 68, 459-465.
 32. Cawoy H, Debois D, Franzil L, De Pauw E, Thonart P, Ongena M. 2015. Lipopeptides as main ingredients for inhibition of fungal phytopathogens by *Bacillus subtilis/amyloliquefaciens*. Microbial Biotechnology 8(2), 281-295.
 33. Chen Y, Fanourakis D, Tsaniklidis G, Aliniaiefard S, Yang Q, Li T. 2021. Low UVA intensity during cultivation improves the lettuce shelf-life, an effect that is not sustained at higher intensity. Postharvest Biology and Technology 172, 111376.
 34. Compant S, Clément C, Sessitsch A. 2010. Plant growth promoting bacteria in the rhizo- and endosphere of plants: Their role, colonization, mechanisms involved and prospects for utilization. Soil Biology and Biochemistry 42(5), 669-678.
 35. Coutinho B.G, Licastro D, Mendonca-Previato L. 2015. Plant-Influenced gene expression in the rice endophyte *Burkholderia kururiensis* M130. Molecular Plant Microbe Interactions 28(1), 10-21.
 36. Creus C.M, Sueldo R.J, Barassi C.A. 2004. Water relations and yield in *Azospirillum*-inoculated wheat exposed to drought in the field. Canadian Journal of Botany 82(2).
 37. Cho S.J, Lee S.K, Cha B.J, Kim Y.H, Shin K.S. 2003. Detection and characterization of the Gloeosporium gloeosporioides growth inhibitory compound iturin A from *Bacillus subtilis* strain KS03. FEMS Microbiology Letters 223(1), 47-51.
 38. Chebotar V.K, Makarova N.M, Shaposhnikov A.I, Kravchenko L.V. 2009. Antifungal and phytostimulating characteristics of *Bacillus subtilis* Ch-13 rhizospheric strain, producer of biopreparations. Applied Biochemistry and Microbiology 45, 419-423.
 39. Chebotar V.K, Malfanova N.V, Shcherbakov A.V. 2015. Endophytic bacteria in microbial preparations that improve plant development

- (review). *Appl Biochemistry and Microbiology* 51(3), 271-277.
40. Chen X.H, Scholz R, Borriss M, Junge H, Mögel G, Kunz S, Borriss R. 2009. Difficidin and bacilysin produced by plant-associated *Bacillus amyloliquefaciens* are efficient in controlling fire blight disease. *Journal of Biotechnology* 140, 38-44.
41. Cherif H, Marasco R, Rolli E, Ferjani R, Fusi M, Soussi A. 2015. Oasis desert farming selects environment-specific date palm root endophytic communities and cultivable bacteria that promote resistance to drought: oasis palm endophytes promote drought resistance. *Environmental Microbiology Reports* 7, 668-678.
42. Chernin L, Chet I. 2002. Microbial enzymes in the biocontrol of plant pathogens and pests. In: Burns R.G, Dick R.P. (Eds.), *Enzymes in the Environment: Activity, Ecology, and Applications*. Marcel Dekker Inc., New York, USA.
43. Chung S, Kong H, Buyer J.S, Lakshman D.K, Lydon J, Kim S.D, Roberts D.P. 2008. Isolation and partial characterization of *Bacillus subtilis* ME488 for suppression of soilborne pathogens of cucumber and pepper. *Applied Microbiology and Biotechnology* 80, 115-123.
44. Díaz-Zorita M, Fernandez-Canigia M.V. 2009. Field performance of a liquid formulation of *Azospirillum brasilense* on dryland wheat productivity. *European Journal of Soil Biology* 45, 3-11.
45. Dimkpa C.O, Merten D, Svatos A, Büchel G, Kothe E. 2009. Siderophores mediate reduced and increased uptake of cadmium by *Streptomyces tendae* F4 and sunflower (*Helianthus annuus*), respectively. *Journal of Applied Microbiology* 107, 1687-1696.
46. Droby S. 2006. Improving quality and safety of fresh fruit and vegetables after harvest by the use of biocontrol agents and natural materials. *Acta Horticulturae* 709, 45-51.
47. Droby S, Wisniewski M, Macarasin D, Wilson C. 2009. Twenty years of postharvest biocontrol research: is it time for a new paradigm? *Postharvest Biology and Technology* 52(2), 137-145.
48. Droby S, Wisniewski M, Teixidó N, Spadaro D, Jijakli M.H. 2016. The science, development, and commercialization of postharvest biocontrol products. *Postharvest Biology and Technology* 122, 22-29.
49. Egamberdieva D, Kucharova Z, Davranov K, Berg G, Makarova N, Azarova T, Chebotar V, Tikhonovich I, Kamilova F, Validov S.Z, Lugtenberg B. 2011. Bacteria able to control foot and root rot and to promote growth of cucumber in salinated soils. *Biology and Fertility of Soils* 47, 197-205.
50. Egamberdieva D, Wirth S.J, Shurigin V.V, Hashem A, Abd Allah E.F. 2017. Endophytic bacteria improve plant growth, symbiotic performance of chickpea (*Cicer arietinum* L.) and induce suppression of root rot caused by *Fusarium solani* under salt stress. *Frontiers in Microbiology* 8, 1887.
51. El-Afry M.M, El-Nady M.F, Belal E.B, Metwaly M.M. 2012. Physiological responses of drought stressed wheat plants (*Triticum aestivum* L.) treating with some bacterial endophytes. *Journal of Plant Production, Mansoura University* 3(7), 2069-2089.
52. Fan H, Ru J, Zhang Y, Wang Q, Li Y. 2017. Fengycin produced by *Bacillus subtilis* 9407 plays a major role in the biocontrol of apple ring rot disease. *Microbiological Research* 199, 89-97.
53. FAO. 2015. Food losses and waste. URL <http://www.fao.org/food-loss-and-food-waste/en/>
54. FAO. 2019. The State of Food and Agriculture 2019. Moving forward on food loss and waste reduction. Rome.
55. Furlan F, Saatkamp K, Volpiano C.G, de Assis Franco F, Santos M.F, Vendruscolo E.C, Guimarães V.F, da Costa A.C. 2017. Plant growth-promoting bacteria effect in withstanding drought in wheat cultivars. *Scientia agraria* 18, 104-113.
56. Garipova S, Shayahmetova A, Lastochkina O, Fedorova K, Pusenkova L. 2020. Effect of inoculation of bean plants by endophytic bacteria *Bacillus subtilis* on the growth of seedlings in model experiments and productivity under the conditions of Southern PreUral. *Agrochemical Herald Journal* 6, 48-53.
57. García-Gutiérrez L, Zeriouh H, Romero D, Cubero J, Vicente A, Pérez-García A. 2013. The antagonistic strain *Bacillus subtilis* UMAF6639 also confers protection to melon plants against cucurbit powdery mildew by activation of jasmonate – and salicylic acid-dependent defense responses. *Microbial Biotechnology* 6(3), 264-274.
58. Gao H, Xu X, Dai Y, He H. 2016. Isolation, identification and characterization of *Bacillus subtilis* CF-3, a bacterium from fermented bean curd for controlling postharvest diseases of

- peach fruit. *Food Science and Technology Research* 22(3), 377-385.
59. Gagné-Bourque F, Bertrand A, Claessens A, Aliferis K.A, Jabaji S. 2016. Alleviation of drought stress and metabolic changes in timothy (*Phleum pratense* L.) colonized with *Bacillus subtilis* B26. *Frontiers in Plant Science* 7, 584.
60. Gotor-Vila A, Usall J, Torres R, Solsona C, Teixidó N. 2017. Biocontrol products based on *Bacillus amyloliquefaciens* CPA-8 using fluid-bed spray-drying process to control postharvest brown rot in stone fruit. *LWT - Food Science and Technology* 82, 274-282.
61. Govender V, Korsten L, Sivakumar D. 2005. Semi-commercial evaluation of *Bacillus licheniformis* to control mango postharvest diseases in South Africa. *Postharvest Biology and Technology* 38(1), 57-65.
62. Gong Q, Zhang C, Lu F, Zhao H, Bie X, Lu Z. 2013. Identification of bacillomycin D from *Bacillus subtilis* fmbJ and its inhibition effects against *Aspergillus flavus*. *Food Control* 36, 8-14.
63. Gowtham H, Singh B, Murali M, Shilpa N, Prasad M, Aiyaz M, Amruthesh K, Niranjana S. 2020. Induction of drought tolerance in tomato upon the application of ACC deaminase producing plant growth promoting rhizobacterium *Bacillus subtilis* Rhizo SF 48. *Microbiological Research* 234, 126422.
64. Gupta V, Bochow H, Dolej S, Dolej S, Fischer I. 2000. Plant growth-promoting *Bacillus subtilis* strain as potential inducer of systemic resistance in tomato against *Fusarium wilt*. *Journal of Plant Diseases and Protection* 145-154.
65. Gupta S, Pandey S. 2020. Enhanced salinity tolerance in the common bean (*Phaseolus vulgaris*) plants using twin ACC deaminase producing rhizobacterial inoculation. *Rhizosphere* 16, 100241.
66. Hassanzadeh K, Aliniaiefard S, Farzinia M.M, Ahmadi M. 2017. Effect of phenological stages on essential oil content, composition and rosmarinic acid in *Rosmarinus officinalis* L. *International Journal of Horticultural Science and Technology* 4, 251-258.
67. Huang D, Wu W, Abrams S.R, Cutler A.J. 2008. The relationship of drought-related gene expression in *Arabidopsis thaliana* to hormonal and environmental factors. *Journal of Experimental Botany* 59(11), 2991-3007.
68. Jamalizadeh M, Etebarian H, Aminian H, Alizadeh A. 2009. Evaluation of *Bacillus* spp. as potential biocontrol agent for postharvest gray mold control on golden delicious apple in Iran. *Journal of Plant Protection Research* 49(4), 405-410.
69. Ji Z.L, Peng S, Zhu W, Dong J.P, Zhu F. 2020. Induced resistance in nectarine fruit by *Bacillus licheniformis* W10 for the control of brown rot caused by *Monilinia fructicola*. *Food Microbiology* 103558.
70. Jiang Y.M, Chen F, Li Y.B, Liu S.X. 2001. A preliminary study on the biological control of postharvest diseases of Litchi fruit. *Journal of Fruit Science* 14(3), 185-186.
71. Kalhor M, Aliniaiefard S, Seif M, Asayesh E.J, Bernard F, Hassani B, Li T. 2018. Enhanced salt tolerance and photosynthetic performance: Implication of γ -amino butyric acid application in salt-exposed lettuce (*Lactuca sativa* L.) plants. *Plant physiology and biochemistry* 130, 157-172.
72. Kasim W.A, Osman M.E, Omar M.N, Abd El-Daim IA, Bejai S, Meijer J. 2013. Control of Drought Stress in Wheat Using Plant-Growth-Promoting Bacteria. *Journal of Plant Growth Regulation* 32, 122-130.
73. Kilani-Feki O, Ben Khedher S, Dammak M, Kamoun A, Jabnoun-Khiareddine H, Daami-Remadi M, Touns S. 2016. Improvement of antifungal metabolites production by *Bacillus subtilis* V26 for biocontrol of tomato postharvest disease. *Biological control* 95, 73-82.
74. Kim H.M, Lee K.J, Chae J.C. 2015. Postharvest biological control of *Colletotrichum acutatum* on apple by *Bacillus subtilis* HM1 and the structural identification of antagonists. *Journal of Microbiology and Biotechnology* 25(11), 1954-1959.
75. Kim G.H, Koh Y.J, Jung J.S, Hur J.S. 2015a. Control of postharvest fruit rot diseases of kiwifruit by antagonistic bacterium *Bacillus subtilis*. *Acta Horticulturae* 1096, 377-382.
76. Kim Y.S, Balaraju K, Jeon Y. 2016. Effects of rhizobacteria *Paenibacillus polymyxa* APEC136 and *Bacillus subtilis* APEC170 on biocontrol of postharvest pathogens of apple fruits. *Journal of Zhejiang University Science B* 17(12), 931-940.
77. Knox O.G, Killham K, Leifert C. 2000. Effects of increased nitrate availability on the control of plant pathogenic fungi by the soil bacterium *Bacillus subtilis*. *Applied Soil Ecology* 15, 227-231.

78. Kolupaev Y.E, Yastreb T.O. 2015. Physiological functions of nonenzymatic antioxidants of plants. *Proceedings of KhNU* 2, 6-25.
79. Krebs B, Ockhardt A, Hoeding B, Bendzko P, Maximov J, Etzel W. 1996. Cyclic peptides from *Bacillus amyloliquefaciens* useful antimycotics, antivirals, fungicides, nematicides etc. DE19641213.
80. Khedher S.B, Kilani-Feki O, Dammak M, Jabnoun-Khiareddine H, Daami-Remadi M, Tounsi S. 2015. Efficacy of *Bacillus subtilis* V26 as a biological control agent against *Rhizoctonia solani* on potato. *Comptes Rendus Biologies* 338, 784-792.
81. Lastochkina O.V, Shirokov A.V, Yuldashev R.A, Pusenkova L.I. 2015. Assessment of influence of bacterial strains of *Bacillus subtilis* in mix with salicylic acid on productivity and infestation of potato tubers. "International scientific-practical conference "Agricultural science in the innovative development of agriculture" Abstracts. Ufa, Russia 1, 112-117.
82. Lastochkina O, Pusenkova L, Yuldashev R, Babaev M, Garipova S, Blagova D, Khairullin R, Aliniaiefard S. 2017. Effects of *Bacillus subtilis* on some physiological and biochemical parameters of *Triticum aestivum* L. (wheat) under salinity. *Plant physiology and biochemistry* 121, 80-88.
83. Lastochkina O.V, Pusenkova L.I, Il'yasova E.Y, Aliniaiefard S. 2018. Effect of *Bacillus subtilis* based biologicals on physiological and biochemical parameters of sugar beet (*Beta vulgaris* L.) plants infected with *Alternaria alternata*. *Agrobiologia* 53(5), 958-968.
84. Lastochkina O. 2019. *Bacillus subtilis*-mediated abiotic stress tolerance in plants. In: *Bacilli and Agrobiotechnology: Phytostimulation and Biocontrol* 2(6). Eds: Islam M.T, Rahman M.M, Pandey P, Boehme M.H, Haesaert G. Springer Nature Switzerland AG.
85. Lastochkina O, Seifi Kalhor M, Aliniaiefard S, Baymiev A, Pusenkova L, Garipova S, Kulabuhova D, Maksimov I. 2019a. *Bacillus* spp.: Efficient biotic strategy to control postharvest diseases of fruits and vegetables. *Plants* 8(4), 7.
86. Lastochkina O, Baymiev A, Shayahmetova A, Garshina D, Koryakov I, Shpirnaya I, Pusenkova L, Mardanshin I, Kasnak C, Palamutoglu R. 2020. Effects of endophytic *Bacillus subtilis* and salicylic acid on postharvest diseases (*Phytophthora infestans*, *Fusarium oxysporum*) development in stored potato tubers. *Plants* 9, 76.
87. Lastochkina O, Pusenkova L, Garshina D, Yuldashev R, Shpirnaya I, Kasnak C, Palamutoglu R, Mardanshin I, Garipova S, Sobhani M, Aliniaiefard S. 2020a. The effect of endophytic bacteria *Bacillus subtilis* and salicylic acid on some resistance and quality traits of stored *Solanum tuberosum* L. tubers infected with fusarium dry rot. *Plants* 9(6), 738.
88. Lastochkina O, Garshina D, Allagulova C, Fedorova K, Koryakov I, Vladimirova A. 2020b. Application of endophytic *Bacillus subtilis* and salicylic acid to improve wheat growth and tolerance under combined drought and Fusarium root rot stresses. *Agronomy* 10, 1343.
89. Leifert C, Li H, Chidburee S, Hampson S, Workman S, Sigee D, Epton H.A, Harbour A. 1995. Antibiotic production and biocontrol activity by *Bacillus subtilis* CL27 and *Bacillus pumilus* CL45. *Applied Microbiology* 78, 97-108.
90. Leelasuphakul W, Sivanunsakul P, Phongpaichit S. 2006. Purification, characterization and synergistic activity of b1,3-glucanase and antibiotic extract from an antagonistic *Bacillus subtilis* NSRS 89-24 against rice blast and sheath blight pathogens. *Enzyme and Microbial Technology* 38, 990-997.
91. Leelasuphakul W, Hemmanee P, Chuenchitt S. 2008. Growth inhibitory properties of *Bacillus subtilis* strains and their metabolites against the green mold pathogen (*Penicillium digitatum* Sacc.) of citrus fruit. *Postharvest Biology and Technology* 48, 113-121.
92. Li Y, Xu S, Jing G, Pan S, Wang G. 2016. *Bacillus subtilis*-regulation of stomatal movement and instantaneous water use efficiency in *Vicia faba*. *Plant Growth Regulation* 78, 43-55.
93. Maksimov I.V, Veselova S.V, Nuzhnaya T.V, Sarvarova E.R, Khairullin R.M. 2015. Plant growth promoting bacteria in regulation of plant resistance to stress factors. *Russian Journal of Plant Physiology* 62(6), 715-726.
94. Maksimov I, Khairullin R. 2016. The role of *Bacillus* bacterium in formation of plant defence: mechanisms and reactions. *The handbook of microbial bioresources*.
95. Mannanov R.N, Sattarova R.K, 2001. Antibiotics produced by *Bacillus* bacteria. *Chemistry of Natural Compounds* 37, 117-123.

96. Morelli M, Bahar O, Papadopoulou K.K, Hopkins D.L, Obradović A. 2020. Editorial: Role of endophytes in plant health and defense against pathogens. *Frontiers in Plant Science* 11, 1312.
97. Nautiyal C.S, Srivastava S, Chauhan P.S, Seem K, Mishra A, Sopory S.K. 2013. Plant growth promoting bacteria *Bacillus amyloliquefaciens* NBRISN13 modulates gene expression profile of leaf and rhizosphere community in rice during salt stress. *Plant Physiology and Biochemistry* 66, 1-9.
98. Naveed M, Baqir Hussain M, Zahir A.Z, Mitter B, Sessitsch A. 2014. Drought stress amelioration in wheat through inoculation with *Burkholderia phytofirmans* strain PsJN. *Plant Growth regulation* 73, 121-131.
99. Niu D.D, Liu H.X, Jiang C.H, Wang Y.P, Wang Q.Y, Jin H.L, Guo J.H. 2011. The plant growth-promoting rhizobacterium *Bacillus cereus* AR156 induces systemic resistance in *A. thaliana* by simultaneously activating salicylate- and jasmonate/ethylene-dependent signaling pathways. *Molecular Plant-Microbe Interactions* 24, 533-542.
100. Numan M, Bashir S, Khan Y, Mumtaz R, Shinwari K, Khan A.L, Khan A, AL-Harrasi A., Plant growth promoting bacteria as an alternative strategy for salt tolerance in plants: a review 2018. *Microbiological Research* 209, 21-32.
101. Okigbo R.N. 2005. Biological control of postharvest fungal rot of yam (*Dioscorea* spp.) with *Bacillus subtilis*. *Mycopathologia* 159, 307-314.
102. Ongena M, Jacques P, Touré Y, Destain J, Jabrane A, Thonart P. 2005. Involvement of fengycin-type lipopeptides in the multifaceted biocontrol potential of *Bacillus subtilis*. *Applied Microbiology and Biotechnology* 69(1), 29-38.
103. Ongena M, Jourdan E, Adam A, Paquot M, Brans A, Joris B, Arpigny J.L, Thonart P. 2007. Surfactin and fengycin lipopeptides of *Bacillus subtilis* as elicitors of induced systemic resistance in plants. *Environmental Microbiology* 9, 1084-1090.
104. Ongena M, Jacques P. 2008. *Bacillus* lipopeptides: Versatile weapons for plant disease biocontrol. *Trends in Microbiology* 16, 115-125.
105. Pandey P.K, Singh M.C, Singh S.S, Kumar M, Pathak M, Shakywar R.C, Pandey A.K. 2017. Inside the plants: endophytic bacteria and their functional attributes for plant growth promotion. *International Journal of Current Microbiology and Applied Sciences* 6(2), 11-21.
106. Partida-Martinez L.P, Heil M. 2011. The microbe-free plant: fact or artifact? *Frontiers in Plant Science* 2, 100.
107. Pereyra M.A, García P, Colabelli M.N, Barassi C.A, Creus C.M. 2012. A better water status in wheat seedlings induced by *Azospirillum* under osmotic stress is related to morphological changes in xylem vessels of the coleoptile. *Applied Soil Ecology* 53, 94-97.
108. Pitzschke A. 2016. Developmental peculiarities and seed borne endophytes in quinoa: omnipresent, robust *Bacilli* contribute to plant fitness. *Frontiers in Microbiology* 7, 2.
109. Pusenkova L.I, Il'yasova E.Y, Maksimov I.V, Lastochkina O.V. 2015. Enhancement of adaptive capacity of sugar beet crops by microbial biopreparations under biotic and abiotic stresses. *Agricultural Biology* 50(1), 115-123.
110. Pusenkova L.I, Il'yasova E, Lastochkina O.V, Maksimov I. V, Leonova S.A. 2016. Changes in the species composition of the rhizosphere and phyllosphere of sugar beet under the impact of biological preparations based on endophytic bacteria and their metabolites. *Eurasian Soil Sciences* 49(10), 1136-1144.
111. Romero D, de Vicente A, Rakotoaly R.H, Dufour S.E, Veening J.W, Arrebola E, Cazorla F.M, Kuipers O.P, Paquot M, PérezGarcía A. 2007. The iturin and fengycin families of lipopeptides are key factors in antagonism of *Bacillus subtilis* toward *Podosphaera fusca*. *Molecular Plant-Microbe Interaction* 20, 430-440.
112. Roychoudhury A, Paul S, Basu S. 2013. Cross-talk between abscisic acid-dependent and abscisic acid-independent pathways during abiotic stress. *Plant Cell Reports* 32, 985-1006.
113. Saleh S.A, Heuberger H, Schnitzler W.H. 2005. Alleviation of salinity effect on artichoke productivity by *Bacillus subtilis* FZB24, supplemental Ca and micronutrients. *Journal of Applied Botany and Food Quality* 79, 24-32.
114. Santoyo G, Moreno-Hagelsieb G, Orozco-Mosqueda Mdel C, Glick B.R. 2016. Plant growth-promoting bacterial endophytes. *Microbiological Research* 183, 92-99.
115. Sarma B.K, Yadav K.S, Singh D.P, Singh H.B. 2018. Rhizobacteria mediated induced systemic tolerance in plants: prospects for abiotic stress management. In: Maheshwari D (ed) *Bacteria in agrobiology: stress management*. Springer, Berlin 225-238.

116. Saikia J, Sarma R.K, Dhandia R, Yadav A, Bharali R, Gupta V.K, Saikia R. 2018. Alleviation of drought stress in pulse crops with ACC deaminase producing rhizobacteria isolated from acidic soil of Northeast India. *Scientific Reports* 8, 3560.
117. Sayed S.A, Atef A.S, Soha E. 2011. Response of three sweet basil cultivars to inoculation with *Bacillus subtilis* and arbuscular mycorrhizal fungi under salt stress conditions. *Natural Sciences* 9(6), 31-36.
118. Seifi kalhor M.S, Aliniaiefard S, Self M, Javadi E, Bernard F, Li T, Lastochkina O. 2018. Rhisobacteria *Bacillus subtilis* reduces toxic effects of high electrical conductivity in soilless culture of lettuce. *Acta horticulturae* 1227, 471-478.
119. Seifikalhor M, Aliniaiefard S, Shomali A, Azad N, Hassani B, Lastochkina O, Li T. 2019a. Calcium signaling and salt tolerance are diversely entwined in plants. *Plant Signaling and Behavior* 14, 1665455.
120. Seifikalhor M, Aliniaiefard S, Hassani B, Niknam V, Lastochkina O. 2019b. Diverse role of γ -aminobutyric acid in dynamic plant cell responses. *Plant Cell Reports* 38, 847-867.
121. Seifikalhor M, Aliniaiefard S, Bernard F, Seif M, Latifi M, Hassani B, Didaran F, Bosacchi M, Rezadoost H, Li T. 2020. γ -Aminobutyric acid confers cadmium tolerance in maize plants by concerted regulation of polyamine metabolism and antioxidant defense systems. *Scientific Reports* 10, 3356.
122. Seifikalhor M, Hassani S.B, Aliniaiefard S. 2019. Seed priming by cyanobacteria (*Spirulina platensis*) and salep gum enhances tolerance of maize plant against cadmium toxicity. *Journal of Plant Growth Regulation* 39, 1009-1021.
123. Sessitsch A, Hardoim P, Döring J, Weilharter A, Krause A, Woyke T, Mitter B, Hauberg-Lotte L, Friedrich F, Rahalkar M, Hurek T, Sarkar A, Bodrossy L, van Overbeek L, Brar D, van Elsas D, Reinhold-Hurek B. 2012. Functional characteristics of an endophyte community colonizing rice roots as revealed by metagenomic analysis. *Molecular Plant Microbe Interactions* 25(1), 28-36.
124. Singh U, Sarma B, Singh D. 2003. Effect of plant growth-promoting rhizobacteria and culture filtrate of *Sclerotium rofsii* on phenolic and salicylic acid contents in chickpea (*Cicer arietinum*). *Current Microbiology* 46, 131-140.
125. Shakirova F.M, Avalbaev A.M, Bezrukova M.V, Fatkhutdinova R.A, Maslennikova D.R, Yuldashev R.A, Allagulova C.R, Lastochkina O.V. 2012. Hormonal intermediates in the protective action of exogenous phytohormones in wheat plants under salinity: a case study on wheat. In: Khan N, Nazar R, I qbal N, Anjum N (eds) *Phytohormones and abiotic stress tolerance in plants*. Springer, Berlin 185-228.
126. Shafi O, Tian H, Ji M. 2017. *Bacillus* species as versatile weapons for plant pathogens: a review. *Biotechnology and Biotechnological Equipment* 31(3), 446-459.
127. Shomali A, Aliniaiefard S. 2020. Overview of signal transduction in plants under salt and drought stresses, In: Hasanuzzaman M, Tanveer M. (Eds.), *Salt and drought stress tolerance in plants: Signaling networks and adaptive mechanisms*. Springer International Publishing, Cham 231-258.
128. Su J, Zhang M, Zhang L, Sun T, Liu Y, Lukowitz W, Xu J, Zhang S. 2017. Regulation of stomatal immunity by interdependent functions of a pathogen-responsive MPK3/MPK6 cascade and abscisic acid. *Plant Cell* 29, 526-542.
129. Sulieman S, Schulze J. 2010. Phloem-derived γ -aminobutyric acid (GABA) is involved in upregulating nodule N₂ fixation efficiency in the model legume *Medicago truncatula*. *Plant Cell Environment* 33(12), 2162-2172.
130. Touré Y, Ongena M, Jacques P, Guiro A, Thonart P. 2004. Role of lipopeptides produced by *Bacillus subtilis* GA1 in the reduction of grey mould disease caused by *Botrytis cinerea* on apple. *Journal of Applied Microbiology* 96(5), 1151-1160.
131. Timmusk S, Abd El-Daim I.A, Copolovici L, Tanilas T, Kännaste A, Behers L, Nevo E, Seisenbaeva G, Stenström E, Niinemets Ü. 2014. Drought-tolerance of wheat improved by rhizosphere bacteria from harsh environments: enhanced biomass production and reduced emissions of stress volatiles. *PLoS one* 9(5), e96086.
132. Turan M, Ekinci M, Yıldırım E, Güneş K, Karagöz K, Kotan R, Dursun A. 2014. Plant growth-promoting rhizobacteria improved growth, nutrient, and hormone content in cabbage (*Brassica oleracea*) seedlings. *Turkish Journal of Agricultural Forestry* 38, 327-333.
133. Thrall P.H, Hochberg M.E, Burdon J.J, Bever J.D. 2007. Coevolution of symbiotic mutualists

- and parasites in a community context. *Trends in Ecology and Evolution* 22(3), 120-126.
134. Ullah A, Sun H, Yang X, Zhang X. 2017. Drought coping strategies in cotton: Increased crop per drop. *Plant Biotechnology Journal* 15, 271-284.
135. van Meeteren U, Aliniaiefard S. 2015. Stomata and postharvest physiology, *Innovations in Postharvest Technology*. CRC Press.
136. Van Meeteren U, Kaiser E, Malcolm Matamoros P, Verdonk J.C, Aliniaiefard S. 2020. Is nitric oxide a critical key factor in ABA-induced stomatal closure? *Journal of Experimental Botany* 71, 399-410.
137. van Loon L.C. 2007. Plant responses to plant growth-promoting rhizobacteria. In: Bakker P.A, Raaijmakers J.M, Bloemberg G, Höfte M, Lemanceau P, Cooke B.M. (eds) *New Perspectives and Approaches in Plant Growth-Promoting Rhizobacteria Research*. Springer, Dordrecht.
138. Vasileva E.N, Akhtemova G.A, Zhukov V.A, Tikhonovich I.A. 2019. Endophytic microorganisms in fundamental research and agriculture. *Ecological genetics* 17(1), 19-32.
139. Verma P, Yadav A.N, Khannam K.S, Kumar S, Saxena A.K, Suman A. 2016. Molecular diversity and multifarious plant growth promoting attributes of *Bacilli* associated with wheat (*Triticum aestivum* L.) rhizosphere from six diverse agro-ecological zones of India. *Journal of Basic Microbiology* 56(1), 44-58.
140. Wang Y, Xu Z, Zhu P, Liu P, Zhang Z, Mastuda Y, Toyoda H, Xu L. 2010. Postharvest biological control of melon pathogens using *Bacillus subtilis* EXWB1. *Journal of Plant Pathology* 92, 645-652.
141. Waewthongrak W, Pisuchpen S, Leelasuphakul W. 2015. Effect of *Bacillus subtilis* and chitosan applications on green mold (*Penicillium digitatum* Sacc.) decay in citrus fruit. *Postharvest Biology and Technology* 99, 44-49.
142. Woo O.G, Kim H, Kim J.S, Keum H.L, Lee K.C, Sul W.J, Lee J.H. 2020. *Bacillus subtilis* strain GOT9 confers enhanced tolerance to drought and salt stresses in *Arabidopsis thaliana* and *Brassica campestris*. *Plant Physiology and Biochemistry* 148, 359-367.
143. Wu L, Huang Z, Li X, Ma L, Gu Q, Wu H, Liu J, Borriss R, Wu Z, Gao X. 2018. Stomatal closure and SA, JA/ET-signaling pathways are essential for *Bacillus amyloliquefaciens* FZB42 to restrict leaf disease caused by *Phytophthora nicotianae* in *Nicotiana benthamiana*. *Frontiers in microbiology* 9, 847.
144. Yáñez-Mendizábal V, Zerriouh H, Viñas I, Torres R, Usall J, de Vicente A, Pérez-García A, Teixidó N. 2012. Biological control of peach brown rot (*Monilinia* spp.) by *Bacillus subtilis* CPA-8 is based on production of fengycin-like lipopeptides. *European Journal of Plant Pathology* 132(4), 609-619.
145. Yang D.M, Bi Y, Chen X.R, Ge Y.H, Zhao J. 2006. Biological control of postharvest diseases with *Bacillus subtilis* (B1 strain) on muskmelons (*Cucumis melo* L. cv. Yindi). *Acta Horticulturae* 712 (2), 735-739.
146. Žiarovská J, Medo J, Kyseľ M, Zamiešková L, Kačániová M. 2020. Endophytic bacterial microbiome diversity in early developmental stage plant tissues of wheat varieties. *Plants* 9, 266.
147. Zhao Y, Shao X.F, Tu K, Chen J.K. 2007. Inhibitory effect of *Bacillus subtilis* B10 on the diseases of postharvest strawberry. *Journal of Fruit Science* 24(3), 339-343.
148. Zhou T, Schneider K.E, Li X. 2008. Development of biocontrol agents from food microbial isolates for controlling post-harvest peach brown rot caused by *Monilinia fructicola*. *International Journal of Food Microbiology* 126, 180-185.
149. Zhou C, Zhu L, Xie Y, Li F, Xiao X, Ma Z, Wang J. 2017. *Bacillus licheniformis* SA03 confers increased saline-alkaline tolerance in Chrysanthemum plants by induction of abscisic acid accumulation. *Frontiers in plant science* 8, 1143.