



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</i> spp.	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).

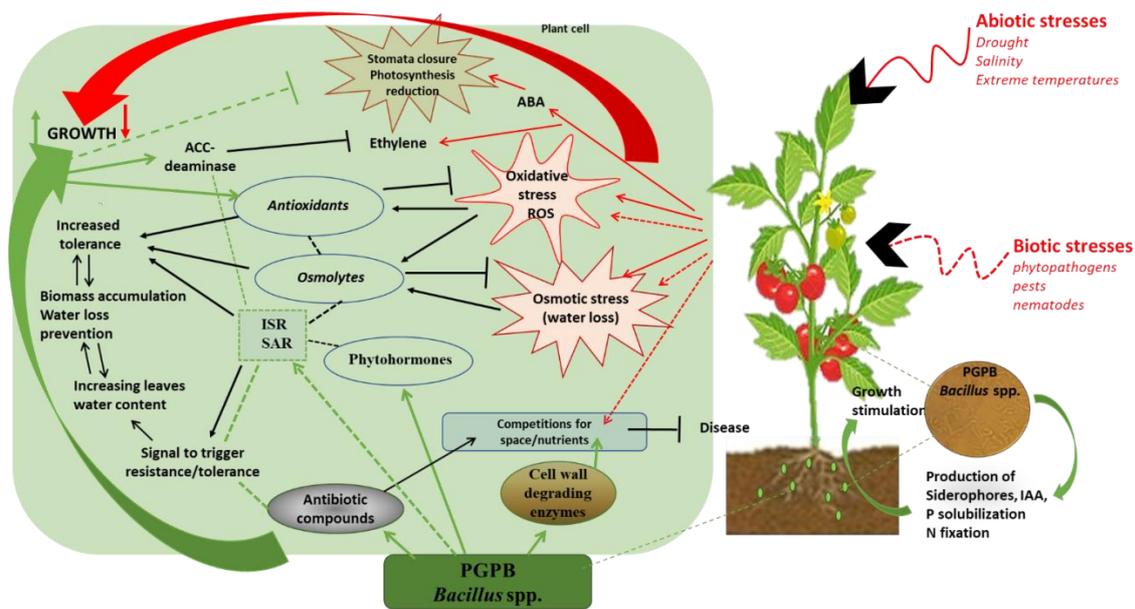


Fig.1. Mechanisms underlying plant growth promoting bacteria-induced plant growth and resistance under biotic and abiotic stresses. ACC-deaminase - 1-aminocyclopropane-1-carboxylic acid deaminase; ABA – abscisic acid; IAA - indole-3-acetic acid; ISR – induced systemic resistance; SAR – systemic acquired 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).

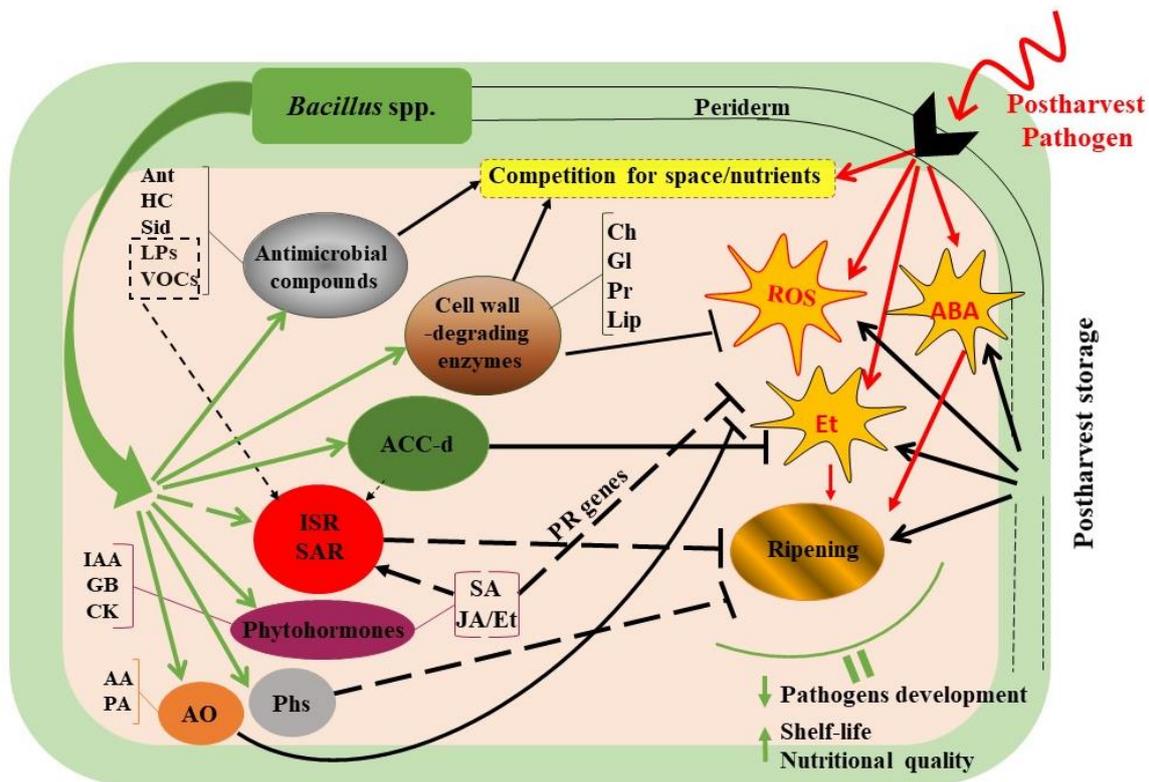


Fig. 2. Mechanisms underlying plant growth promoting bacteria-induced resistance in harvested fruits, vegetables, and flowers in response to biotic stresses. AA - ascorbic acid, ABA - abscisic acid, ACC-d - 1-aminocyclopropane-1-carboxylate deaminase, Ant - antibiotics, AO - antioxidants, Ch -chitinases, 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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