Plant Growth Promoting Bacteria

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Contributor: Kumar Pranaw

PGPB can be used effectively under conditions of nutrient deficiency and are gradually replacing fertilizers. As phytostimulants, PGPB can increase plant growth and crop yield. Some of these bacteria can suppress phytopathogens by producing various metabolites, which is referred to biocontrol properties.

Keywords: abiotic stress ; salinity stress ; drought stress ; plant-microbe interaction ; sustainable agriculture

1. Introduction

Soil, as an extremely heterogeneous environment, contains many different microorganisms with different properties. Plant health and soil fertility require balance and proper cooperation with beneficial microbes, especially bacteria [1]. In the natural environment, bacteria may occur freely in bulk soil from where they can be transferred to the rhizosphere, or internal parts of plants as endophytes [2][3]. The phytomicrobiome is a whole, well-structured community of all microorganisms in a given plant, associated with the host [2][3][4][5]. The rhizosphere, a thin film of soil around the roots, is the primary location of ion uptake for plants, simultaneously depositing nutrients and signaling molecules into this zone [6][7]. This special mixture secreted by plant roots contains low-molecular weight organic substances, such as carbohydrates, amino acids, fatty acids, organic acids, vitamins and a small amount of secondary metabolites [8][9]. The extremely carbon-rich root exudates create a unique space with maximum bacterial activity compared to the bulk soil [7][10]. The nature of secreting exudates and various genetic regulations can influence the structure of bacterial community in the soil [2]. This special recruitment of certain microbes enables the achievement of tangible benefits that would not be possible during solitary growth of the plant [11].

Climate change, despite its remarkable stability and repetition, is embedded in the Earth's past. However, human actions are significantly accelerating these changes in global climate patterns [2][3]. The predominant signs of climate change are elevated mean surface temperature, ice melting, sea level rise and extreme weather events [3][4]. As a result of these rapid global alterations, crops are increasingly facing abiotic stresses, mainly drought, salinity and heat stress [2][9][12][13]. The demand for food is constantly increasing due to the growing population. Therefore, farmers have started using chemical pesticides and fertilizers in high doses to increase agricultural production [9][13]. Altered soil properties and structure due to climate change, along with artificial irrigation and unbalanced use of chemicals, are leading to the destruction of microbial communities in arable soils [11][14]. Since 1961, a nine-fold increase in fertilizer consumption has been observed worldwide [14]. The negative impact on the diversity of bacteria in the wheat rhizosphere under inorganic fertilizers has been established by Reid et al. [15]. According to model studies by Ortiz-Bobea et al. , anthropogenic climate change has significantly affected global agricultural productivity [16]. The reduction in the amount of beneficial microorganisms and the disruption of nutrient cycling in the ecosystem has led to reduction in yields of about 21% since 1961. Nowadays, most farmers still use inorganic fertilizers, which creates a vicious cycle [16][17]. Additionally, the natural biocontrol properties of soil may become severely limited under these conditions, exposing plants to various diseases. Similarly, the host-pathogen relation may shift, as a result of global climate change [4].

Undoubtedly, the spread of land use nowadays is incomparably huge as opposed to the past. Three-quarters of non-ice land, that is, about 17 Mkm 2, is actively utilized by humans, of which around 13% is cultivated, and the value is constantly growing. It has been estimated that since 1961 there has been a 3.5-fold increase of farmlands production and 2.5-fold increase of animal products [14]. As agriculture develops, the global food supply is rising, along with the growing trend of meat and vegetable oil consumption [8][14][18].

2. Climate Change and Its Impact on Agriculture

Temperature is a key ecological factor with a direct impact on physiological processes and plant development. An increase in temperature has a positive effect on faster development of green mass and a shorter duration of cultivation [19]. However, a sharp drop or rise in temperature damages the plant cells, which ultimately leads in an overall lower yield

[19][20]. Zhao et al. have reported that yield losses in maize, wheat, rice and soybean crops ranged from 3.1% to 7.4% per one degree Celsius increase in global mean temperature [19]. Other studies found a 6% and 4% decline in wheat and maize yields, respectively, over a 29-year period of warming trends [21]. Heat stress due to increased temperature is a limiting factor on photosynthesis, especially for C 3 crops such as rice and wheat, but also for C 4 plants, maize and sugarcane crops [19][21][22][23]. In addition, temperature increase affects plants through changes in humidity. Lowering the water vapor content in the air leads to water loss from the plant, causing stomata to close and reducing the efficiency of photosynthesis [24][25]. Prolonged high temperatures lead to drought and water stress in plants, which in turn leads to water scarcity [25].

Too high a concentration of Na + ions in the roots causes not only osmotic stress, but also has a negative impact on the transport of K + ions to plant cells. Moreover, a very high Na + ion concentration in plant cells results in various physiological disorders, such as reduced flowering or fruiting [13]. The following metabolic processes are very sensitive to increased salinity: transport of electrons, phosphorylation, photosynthesis and photorespiration [26][27]. Salt stress significantly lowers the efficiency of photosynthesis due to its multi-level action. The uptake and accumulation of Na + and Cl - can act as photosynthesis inhibitors which disrupt photosynthesis and reduce the production and size of leaves, which can lead to plant death [13][28]. Nevertheless, the toxic effect of salts is less harmful than osmotic stress. The higher concentration of ions in the environment is accompanied by their more intensive uptake by plants. This slightly reduces the water potential of the roots and, as a result, stimulates the water uptake by the plant [29][30].

Water uptake by a plant occurs vertically upward through the steam as a result of the water potential gradient between the soil and the plant and within the plant. Lack of water in the soil leads to a decrease in the water potential in the soil and thus to a decrease in water uptake [28]. Thus, drought conditions generate information that is transmitted to the plant's leaves via ABA and other hydraulic signals. As a result, the plant protects itself against these conditions through a number of processes, such as closing stomata [17][28]. This is to prevent the water potential inside the plant from being reduced, which would only exacerbate the growing problem. One of the measures of soil water potential reduction is stomatal conductance [28]. Soil water availability can be expressed as soil water content or soil water potential. While soil water content is the amount of water present, water potential is the amount of water available to the plant [31][32]. Thresholds of available soil water to plants vary widely and depend on atmospheric conditions, soil type and plant species [32].

Drought tolerance is usually the result of many biochemical and physiological adaptations, which consequently allow the plant to maintain its desired size and yield despite unfavorable environmental conditions. However, in the case of long-term or sudden changes, the plant is unable to cope and needs external help to survive.

3. Plant Growth Promoting Bacteria (PGPB)

The beneficial effects on the plant through interaction with PGPB can be achieved both directly as well as indirectly [10][33]. Direct mechanisms are based on the production of plant growth promoting substances or biofertilization by mobilizing mineral soil components [34]. These processes have a decisive influence on the condition of the plant and their development [6][9][35][36][37]. Reducing the impact of plant diseases caused by pathogens, mitigating abiotic stress or inducing systemic resistance in competition for nutrients and niches are categorised as indirect mechanisms [6][38]. The most common and successful PGPB belong mainly to the genera Agrobacterium , Azospirillum , Azotobacter , Bacillus , Burkholderia , Pseudomonas , Streptomyces and Serratia [39][40].

Phytohormones produced by bacteria can act as plant growth regulators involved in plant development, physiology and immunity [41]. PGPB can synthesize auxins, gibberellins, cytokinin and abscisic acid [2][31][32][42][34]. Auxins, especially indole-3-acetic acid (IAA) produced by PGPB, can stimulate root growth, nodulation and cell proliferation [7][43]. Synthesis of auxin has been demonstrated several times by different strains, mainly represented by the genera: Bacillus , Burkholderia , Serratia , Aeromonas and Azospirillum [34]. Some PGPB are also cytokinin and gibberellin producers, but further research is needed to determine the role of these bacterial hormones in plant growth [2][13][44]. It has been presented that Azospirillum strains producing gibberellin resulted in growth promotion when inoculated into maize roots [45]. In addition, Parmar et al. demonstrated the ability to produce gibberellin in fluorescent Pseudomonas strains [44].

Abiotic stresses, as mentioned earlier, adversely impact on physical-chemical soil properties and microbial communities [46][47][48]. As a selection factor, long-term abiotic stress contributes to the evolution of specific microorganisms, able to survive in adverse environmental conditions [46][49]. Bacteria belonging to particular species differ in stress tolerance. Although some species do well with abiotic stresses, because of individual properties, only selected strains are able to live under particular conditions [50][51]. Some of the PGPB are able to survive and proliferate under stressful conditions due to different adaptation mechanisms [13]. In this work, we refer to these microbes as abiotic stress tolerant growth promoting bacteria (AST-PGPB). Normally, microorganisms require a longer period of adaptation under rapid environmental changes when interacting with the host plant. The composition of root exudates tends to change under particular stressful conditions. Synthesis of particular substances can stimulate the mechanisms of counteracting abiotic stress in microorganisms [50][52]. Therefore, selected biochemical compounds may participate in the close interaction between microbes and plants by activating specific microbial stress genes. Such plant-associated microorganisms generally adapt much faster to new stress conditions, which supports microbial survival. This unusual relation makes AST-PGB an efficient tool for promoting plant growth under abiotic stress conditions [18][48]. It has been reported that some AST-PGPB are even more active under harsh environmental conditions [39][40]. Nagaraju et al. demonstrated that the solubilization of zinc compounds decreases significantly with increasing salinity [53]. In addition, selected AST-PGPB may not exhibit PGPB properties or promote plant growth under standard conditions. However, when used under harsh conditions, they may exhibit growth-promoting and stress-alleviating effects [18][39][54].

Some of AST-PGPB bacteria exposed to abiotic stress conditions are capable of producing VOCs. These lipophilic, low molecular weight compounds are often produced by microbes as regulators of various properties [43][55]. Plants can use these substances as indicators, by which they recognize microbial species of with which they interact profitably [56]. Mainly, the production of acetoin, butanediol, 1,3-propanediol, geosmin and dimethyl disulfide by bacteria have been reported [56][57]. However it is estimated that thousands of such compounds are produced by different bacteria, such as alcohols, alkanes, alkenes, aldehydes, esters, ketones, organic acids or sulfur compounds [58].

4. PGPB and Its Role in Inducing Different Abiotic Stress Tolerance in Plants

Selected salinity-tolerant bacteria are able to produce hormones, ACC deaminase, osmoprotectants or secondary compounds, such as EPS and VOCs, under high-salinity conditions [59][60][41][61]. AST-PGPB inoculation may lead to positive adaptive responses of plants to salinity stress. This can occur through several mechanisms, including altered hormone production by the plant, increased nutrient uptake, lowering water stress, maintainance of favourable K + /Na + ratio or osmotic adjustment[39][56][41]. Several genera are involved in the successful control of salinity stress in crops, such as Bacillus , Pseudomonas , Agrobacterium , Streptomyces or Ochromobacter [39][62][63][64]. Many studies have been conducted to verify the prevalence of salinity-tolerant strains. The dominance of 8% NaCl-tolerant Bacillus sp. in the wheat rhizosphere was observed [65]. Zhang et al. reported that of 305 bacteria isolated from paddy soil in Taoyuan, China, 35.7%, 15.1% and 4.9% of the strains were able to grow in media with 5%, 10% and 15% NaCl concentrations, respectively [66]. Most of these isolates exhibited plant growth promoting potential in rice cultivation under high salinity stress. Moreover, phylogenetic analysis of 74 selected isolates revealed that most of bacteria belonged to the order Bacillales. However, one of the best salinity tolerances for field strains, up to 20%, was found for Klebsiella sp. IG3 isolated from wheat rhizosphere [67]. In addition, it has been reported that multispecies inoculum consisting of endophytic and rhizosphere PGPB under salinity stress may increase crop yield [13].

Bacterial GA and ABA increased leaves compared to the control treated with these hormone inhibitors under drought stress [68]. The experiment proved a significant role of these hormones in plant growth and drought tolerance. In addition, JA plays a role in alleviating drought stress by increasing antioxidant activity. Therefore, bacteria increasing JA hormone production may enhance drought tolerance [69]. P. putida H-2-3 mitigated the drought and salinity stress effects on soybean by GA production ability. Soybean inoculated P. putida H-2-3, compared to the control under drought conditions, exhibited slightly better chlorophyll content (1.2%), but primarily a greater shoot length (13.6%) and plant fresh weight (12.8%) [13]. Sarma and Saikia have reported that mungbeans inoculated with Pseudomonas aeruginosa GGRJ21 under 0.73 MPa drought conditions enhanced their biomass and growth in field conditions compared to control [70]. Bacterial inoculation promoted root length in the plants by 127% and shoot length by 42% under water stress conditions. The elongation of the roots and shoots was possible due to IAA production and the stress reduction effects through the ACC deaminase activity. Moreover, bacterial up-regulated transcription of stress responsive genes, which contributes to the plant stress tolerance [70]. Cytokinin as a natural plant hormone supports the young plant, thus preventing leaves scarcity. However, its synthesis during drought is limited [69]. Inoculation of cytokinin-producing strain B. subtilis on Platycladus orientalis elevated cytokinin in shoots under drought stress [71]. It was noted that GA plays a crucial role in the control of the degree of opening of the stomata, and therefore is responsible for the process of stomatal transpiration. In times of drought, access to water is negligible, so closing the apparatuses may reduce water losses [72]. Bacterial inoculation elevated ABA and reduced drought stress. Cucumber inoculated with of P. putida enhanced shoot length and biomass due to higher endogenous GA production in plants [13]. Azosprillum brasilense Sp245 inoculation elevated ABA and reduced drought stress in Arabidopsis [73]. Phyllobacterium brassicacearum STM196 inoculated with rapeseed increased osmotic stress tolerance under drought stress due to elevated ABA concentration. Moreover, A. brasilense due to nitric oxide production enhanced adventitious root development in tomato, which could be another mechanism of drought stress alleviation [74].

Maize inoculated with A. brasilense enhanced proline accumulation, plant water content, biomass and leaves area of plant under drought stress [73]. Additionally, it has been reported that wheat inoculated with A. brasilense Sp245 under drought conditions increased yield, mineral uptake and water content in the plant [75]. Similarly, maize inoculated with P. putida GAP-45 increased relative water content due to proline accumulation under drought stress [76]. Increased proline accumulation was also observed in Lavandula dentata inoculated with B. thuringiensis and tomato inoculated with Bacillus polymyxa [77][78].

Low concentrations of ethylene have a positive effect on adventitious root development and fruit ripening, while high production of ethylene under abiotic stress conditions, including drought, leads to many harmful effects, such as inhibition of root and shoot growth, defoliation and premature senescence [6][79]. Saikia et al. reported on the potential benefits of employing a consortium of ACC-deaminase generating bacteria to alleviate drought stress in black gram and garden pea [62]. Other plants, such as tomato and pepper, inoculated with ACC deaminase producing Achromobacter piechaudii ARV8, showed beneficial impacts, such as increased growth, particularly fresh and dry weights, under drought stress [80]. Garden pea inoculated with the ACC deaminase producer P. fluorescens resulted in longer roots, and thus increased water uptake, under drought stress [81].

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