Bacterial Amelioration of Plant Drought and Salt Stress

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Soil bacteria can express different plant-beneficial activities, inoculation of plants with one or more non-antagonistic microorganisms, belonging to the same or different species, or including both prokaryotic and eukaryotic organisms, can often facilitate plant growth. In fact, the lack of one plant beneficial activity in one strain can sometimes be overcome if another microorganism expresses this specific physiological trait. Moreover, the combination of diverse plant growth-promoting microorganisms (PGPM) offers a wide range of positive activity to a plant, including the enhancement of plant growth, reduced susceptibility to soil-borne diseases, increased yield, and improved seed and fruit nutritional value.

sustainable agriculture plant growth-promoting bacteria (PGPB) salt stress drought stress

1. Drought and Salt Stress

Plants that are grown in the field under natural conditions are typically subjected to a wide range of both biotic and abiotic stresses, any one of which may significantly inhibit plant growth and development [1]. Biotic stress factors that are inhibitory to plant growth and development include viruses, nematodes, insects, phytopathogenic bacteria, and phytopathogenic fungi. In addition, abiotic stress factors that are detrimental to plants include extremes of temperature, excessively high or low light conditions, flooding, drought, high salt, toxic metals, organic contaminants, and excessive radiation. It was focused on the effects and remediation of drought and salt stress, two of the most problematic abiotic stresses as far as plant growth is concerned.

Soil salinity and drought are enormous global problems for the growth of agricultural plants. Worldwide drought has increased dramatically in recent years because of the increasing impacts of climate change (https://climate.nasa.gov/news/3117/drought-makes-its-home-on-the-range/, accessed on 5 January 2022; https://www.c2es.org/content/drought-and-climate-change/, accessed on 5 January 2022). Soil salinity is not only affected by climate change but is especially problematic for crops that require irrigation. Because of the lack of sufficient water (for example, drought) in many locations, some farmlands are under-irrigated, causing salt (from the irrigation water) to accumulate in the soil. In this case, the salt remains in the soil when the irrigation water is either utilized by plants or is lost to evaporation. Moreover, the majority of the world’s salt-inhibited soils are found in arid or semi-arid climates (https://www.fao.org/global-soil-partnership/resources/highlights/detail/en/c/1412475/, accessed on 5 January 2022). Compounding the negative effects of drought, the high salt levels that result from irrigation are inhibitory to the growth of many plants. At present, it is estimated that >900 million hectares or ~20% of the world’s cultivated land mass is negatively impacted by high levels of salt. Moreover, a significant fraction of the global land mass used for the growth of irrigated crops is somewhat adversely affected by high levels of salinity.

The initial responses of most plants to drought and salinity are similar; both responses are largely due to water stress within the plant [2][3]. When plants are first exposed to high levels of salt, a decrease in their growth rate occurs. This is often followed by a slow recovery to a lower growth rate. Subsequently, following the continued uptake of salt by plants, sodium ions are translocated through the xylem to the plant shoots, with leaves and shoots eventually accumulating high levels of sodium ions. The toxicity of accumulating sodium ions in plants is generally considered to be a function of the excessive amounts of sodium ions that compete with potassium ions for the binding sites that are necessary for plant cellular functioning. This abiotic stress results in the generation of a number of reactive oxygen species within the plant [4], which in turn can cause electrolyte leakage from plant cells, plant cell membrane lipid peroxidation, an increase in photorespiration, a decrease in transpiration, eventual pollen sterility, and a decrease in the plant’s rate of photosynthesis, all of which negatively affect the plant yield and quality.

Plants are able to use a range of mechanisms to deal with salt stress [1][2], including (i) selective accumulation (in vacuoles) or exclusion of sodium ions, (ii) modulation of the root uptake of sodium ions and the subsequent transport of these ions into leaves, (iii) compartmentalization of sodium ions at the plant cellular level, (iv) synthesis of a variety of compatible solutes such as trehalose and proline, (v) modification of plant cell membranes, (vi) synthesis of various antioxidative enzymes, including superoxide dismutase and peroxidase, and (vii) modulation of some plant hormone levels, including auxin, cytokinin, and ethylene. Moreover, the salt tolerance of any particular plant species is often a function of the specific salt tolerance of the cultivar of the plant being examined, the growth phase of the plant, the soil composition, the plant’s health, the presence and nature of plant pathogenic organisms, the presence of specific rhizospheric or endophytic plant growth-promoting bacteria (PGPB), and the presence of mycorrhizae [1].

In considering the different PGPB mechanisms that can be employed, it is necessary to bear in mind that many of these activities and their regulation are interconnected. Moreover, different PGPB contain different sets of genes that enable them to provide a range of varied protective responses against the inhibitory effects of a range of abiotic (and biotic) stresses, including drought and salinity. In addition to the more direct effects of PGPB on plants, many PGPB can also modify plant gene expression, thereby increasing the plant’s synthesis of stress protective agents. Thus, for example, some PGPB may promote an increase in the plant’s production of “water-structuring” metabolites (osmolytes), such as betaine, proline, and trehalose, and the synthesis of reactive oxygen detoxifying enzymes, such as superoxide dismutase and catalase [1].

The ability of PGPB to overcome the effects of salt stress on plant growth has been focused to a much greater extent than the ability of PGPB to ameliorate drought stress. This somewhat disparate focus may reflect the fact that salt stress is technically easier to impose in a laboratory setting and is of more universal interest than drought stress. This notwithstanding, numerous have been reported success in using PGPB to ameliorate some of the deleterious effects of both salt and drought stress.

Interestingly, drought and/or salt stress often increases the sensitivity of many plants to various phytopathogens, often by decreasing the plant's ability to effectively mount an attack against the pathogen. However, it has been observed that PGPB isolated from salt- or drought-stressed soils, in addition to the previously mentioned ability to protect plants against these abiotic stresses, can frequently effectively protect plants against the damage caused by many different fungal phytopathogens [5][6][7].

2. Plant Growth-Promoting Bacteria

PGPB direct promotion of plant growth by may occur by the bacterium, providing a plant with one or more phytohormones, including auxin, cytokinin, or gibberellin, by improving the ability of a plant to acquire soil nutrients including iron, solubilized phosphate, zinc or potassium, and fixed nitrogen. PGPB that express the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase can lower plant ACC and ethylene levels and thereby increase a plant's tolerance to a wide range of environmental ethylene-generating stresses [8][9][10][11][12]. The phytohormones, cytokinin, auxin, and ethylene levels have all been directly implicated in playing a role in protecting plants from inhibition by drought and salt stress [1][2][11][13][14].

3. Groups of Microorganisms to Lower Plant Drought and Salt Stress

Since bacteria can express different plant-beneficial activities, inoculation of plants with a combination of two or more non-antagonistic microorganisms, belonging to the same or different species, or including both prokaryotic and eukaryotic organisms, can often lead to additive or synergistic effects in the promotion of plant growth. In fact, the lack of one plant beneficial activity in one strain can sometimes be overcome if another microorganism expresses this specific physiological trait [15][16]. Moreover, the combination of diverse plant growth-promoting microorganisms (PGPM) offers a wide range of positive activity to a plant, including the enhancement of plant growth, reduced susceptibility to soil-borne diseases, increased yield, and improved seed and fruit nutritional value. The commercialization of groups of PGPM as biofertilizers and biocontrol agents represents the bottleneck of the full process [17][18]. However, as demonstrated by the large number of scientific papers recently published on this topic, the use of microbial consortia is becoming a reliable tool to support plant growth in stressed environments, especially those characterized by an excess of salt [19][20][21][22] or a deficiency of water [23][24][25].

3.1. Bacterial Consortia

Bacterial consortia may be classified as either simple or complex. In simple consortia, all of the bacterial strains are inoculated in a bioreactor at the same time, while in a complex consortium, the bacterial growth occurs in separate bioreactors [26]. Once the strategy of employing a simple consortium has been decided upon, it should be considered that the metabolism of each inoculated bacterial strain affects the growth and physiology of the other co-existing strains, leading to a plethora of possible interactions, ranging from neutral, to positive (cooperation, synergism, commensalism), to negative (amensalism, competition, antagonism). Although the occurrence of one or the other type of interactions is usually finely monitored and regulated during the scale-up of the fermentation process, the issue of the strain's compatibility plays a pivotal role in the final result [27]. For, example, in *Pseudomonas koreensis* S2CB45 (which was isolated from the surface sterilized spore of a mycorrhizal fungi) and *Microbacterium hydrothermale* IC37-36 (which was isolated from a rice spermosphere), the expression of plant-beneficial traits such as ACC deaminase, IAA, and cytokinin was higher when these PGPB were co-cultured rather than grown separately. Consequently, when this consortium was used to inoculate red pepper plants grown at two salt stress levels, these bacterial strains reduced ethylene emission by 20% compared to uninoculated plants, lowered ROS accumulation, and increased activity of antioxidant enzymes [19].

Especially for those consortia intended for use as plant growth promoters in saline or arid environments, the sampling site from which the bacterial strains are isolated is key. Since autochtonous plants growing in arid environments have co-evolved with their associated microbiota, it is commonly thought that selecting bacterial strains from these specific environments may help to obtain well-adapted bacterial strains with high tolerance to stress as well as long survival and persistence in open field conditions [28][29].

Mansour et al. [30] examined the effects of either the single or double inoculation of five faba bean cultivars with strains *R. leguminosarum* bv. viciae USDA 2435 and *P. putida* RA MTCC5279 on the growth and health of these plants treated to (i) optimal watering, (ii) moderate watering, or (iii) severe drought conditions. While the water deficiency reduced the synthesis of photosynthetic pigments and enhanced the production of antioxidant enzymes and osmoprotectants to a different extent according to the drought sensitivity of the cultivar, plant inoculation with the bacterial strains led to increased seed yield and crop water productivity.

Similarly, among 89 strains originally from the rhizosphere or endosphere of two Algerian autochthonous halophytic plants (*Suaeda mollis* and *Salsola tetrandra*), three bacterial strains, i.e., *Bacillus atropheus* (BR5, OR15, and RB13), were selected based on plant growth-promoting traits (IAA, ACC deaminase, nitrogen fixation, and phosphate solubilization), antifungal activity, and tolerance to environmental conditions (pH, PEG, and NaCl). The bacterial strains were used to inoculate *A. thaliana* and durum wheat alone or in combination under salt stress conditions. Overall, the data obtained indicate that bacterial inoculation of both plant species increased plant growth under normal conditions. When wheat plants were cultivated in soils characterized by three salinity levels, inoculation with the consortium was the most efficient strategy for increasing growth compared to control plants. Finally, inoculation with the consortium increased chlorophyll and carotenoid contents while lowering proline content, lipid peroxidation, and the activities of antioxidant enzymes in treated plants, suggesting that the bacterial treatments limit the damages induced by salt stress [22].

3.2. Bacteria Plus Fungi (Including AMF)

Consistent with the fact that plant microbiota includes a wide variety of different microorganisms, the effects of consortia involving bacterial strains associated with arbuscular mycorrhizal fungi (AMF) and other non-obligate symbiotic fungi on plant growth under arid conditions is a powerful tool, where each microorganism potentiates the bioprotection against the effects of various abiotic stresses on the plant [14]. AMF are common plant-beneficial fungi that typically form a symbiotic relationship with the roots of ~80–90% of all land plants, colonizing plant roots intracellularly. AMF enter the root cortical cell walls, and once inside these cells, form obligate branched intracellular fungal structures (arbuscules), where an exchange of nutrients between the plant and the beneficial fungus takes place. In this exchange, the plant provides the fungus with both fixed carbon and nitrogen, and in exchange, the fungus provides the plant with an effectively increased root system and a significantly increased ability to take up water and nutrients from the soil.

The work of several researchers has highlighted the occurrence of additive and synergistic effects between AMF and PGPB [15], with PGPB behaving as mycorrhizal helper bacteria and thus favoring the establishment of the mycorrhizal symbiosis. Even more complex is the interrelationship involving legumes, rhizobia, and AMF, where the AMF can favor nodule formation, while rhizobia may reduce mycorrhizal hyphal development [31]. On this latest point, contrasting results have been obtained by Igiehon and Babalola [32], who assessed the effects of a combination of rhizobia species and AMF on the growth of soybean under drought stress. Based on their results, co-inoculation of soybean plants with the bacteria *Rhizobium* sp. R1 and *R. cellulosilyticum* R3, together with a consortium of AMF (consisting of *Paraglomus occulum*, *Gigaspora gigantea*, *Funneliformis mosseae*, *Claroideoglomus etunicatum* and *Rhizophagus clarus*), improved the growth and yield of soybean plants that were exposed to 40% water stress, leading to enhanced leaf relative water content and proline concentration. Moreover, mycorrhizal plants that were inoculated with rhizobia displayed the greatest number of fungal spores and mycorrhizal colonization intensity of all the water regimes, revealing that the rhizobia and AMF consortium can positively interact and represent a valuable tool in sustainable agriculture.

A large number of factors can affect the tripartite relationship between the host plant, mycorrhizal fungi, and PGPB strains, ranging from the host plant and AMF species involved to the chemical and physical parameters of the growth substrate(s) [33][34]. For example, Veselaj et al. [35] reported that in legumes the relationships occurring among AMF, PGPB, and rhizobia are dependent both on the species of microorganisms involved and the level of salinity. Inoculated pea plants were grown at two different levels of salt stress, with two AMF (*Rhizophagus irregularis* and *C. claroideum*) and/or two PGPB, one of them being a rhizobial strain (*Rhizobium leguminosarum*) and *Burkholderia* sp. When grown under optimal conditions, the plant growth parameters were improved by inoculation with *R. irregularis* and bacteria (*R. leguminosarum* and *Burkholderia* sp.) or by the combination of the AMF (*R. irregularis* + *C. claroideum*) with each type of bacteria. While the plant growth was reduced by the salt stress, inoculation with *R. irregularis* led to better vegetative development and higher productivity than with *C. claroideum*. Moreover, under salt stress, pea plants treated with *Burkolderia* sp. increased vegetative growth more efficiently than *R. leguminosarum*. In this experiment, the best results, in terms of plant growth and productivity, were observed with plants inoculated with both AMF the rhizobia strain.

In addition to AMF, mixed bacterial/fungal consortia can include other microfungi, such as isolates of *Trichoderma* species and the root endophyte *Serendipita indica* (previously classified as *Piriformospora indica*). While *Trichoderma* spp., and especially *Trichoderma harzianum*, is mainly known for its mycoparasistic behaviour mediated by chitin degradation [36], *S. indica* is a root endophyte mimicking AMF, able to grow in pure culture and improve nutrient uptake, increasing disease resistance and stress tolerance to environmental conditions [37]. Recently [38], lettuce and tomato plants were cultivated in the presence of different salinity levels and inoculated with two commercial biostimulants, one containing *Bacillus amyloliquefaciens*, *B. brevis*, *B. circulans*, *B. coagulans*, *B. firmus*, *B. halodenitrificans*, *B. laterosporus*, *B. licheniformis*, *B. megaterium*, *B. mycoides*, *B. pasteurii*, *B. subtilis*, and *Paenibacillus polymyxa*, and the other *Glomus* spp., *Agrobacterium radiobacter*, *Bacillus subtilis*, *Streptomyces* spp., and *Tricoderma* spp. While uninoculated plants showed symptoms related to salinity, plants inoculated with the two formulations showed increased biomass, leaf number, and leaf area and were less sensitive to salinity stress. Comparing the efficacy of the two commercial formulations, the inoculum with the consortium containing AMF was more effective than the one based exclusively on Bacillus species.

Notwithstanding the good results obtained inoculating plants with *S. indica*, both under optimal and drought/salt stressed conditions [39][40][41][42][43], combinations of *S. indica* and PGPB have not always yielded positive results. Thus, the possibility of using this fungus in consortia with PGPB has been shown to be effective only in studies aimed at increasing plant disease resistance [44].

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