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ROLE OF PLANT-MICROBE INTERACTIONS ON ABIOTIC STRESS TOLERANCE IN PLANTS: A REVIEW

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Abstract

Plants are continuously exposed to a wide array of environmental stresses. Abiotic stress is one of the foremost limiting factors that are responsible for low agricultural productivity. The incidence of extreme events like prolonged drought, salinity, intense rain and flooding, heat wave and frost damage, metal toxicities in problematic soils are increasing day by day under the scenario of changing climate. Crop plants need to acclimatize against adverse external pressure created by environmental and edaphic conditions with their intrinsic biological mechanisms. Here, microorganisms can come to rescue in an economical and ecofriendly manner in order to help plants for better fitness against abiotic stressors. Various kinds of local and systemic responses that improve metabolic capability of the plants to fight against abiotic stresses are evoked by their interactions with compatible microbes. A number of complex mechanisms for plant-microbe interaction take place within the plant cellular system. Plant- associated microorganisms, such as mycorrhizal fungi, nitrogen-fixing bacteria, and plant growth-promoting rhizobacteria (PGPR), are well recognized for their roles in enhancing crop productivity and providing stress tolerance. Response to abiotic stresses in higher plants is influenced by microorganisms through different mechanisms like induction of osmo-protectants and heat shock proteins, etc. in plant cells; besides, influencing the physico-chemical properties of rhizospheric soil through production of exopolysaccharides and formation of biofilm. Majority of studies dealing with bacterially mediated tolerance to abiotic stresses focused on merely evaluating the plant growth-promoting effects; however, the modes of action largely remain elusive. So, it is high time to understand the roles and mechanisms of plant-microbe interactions *vis-à-vis* abiotic stress tolerance in host plants at the cellular level through future study.

Keywords: abiotic stress, plant-microbe interaction, PGPR, tolerance, exopolysaccharides

Introduction

One of the most vulnerable sectors owing to climate-change is agriculture. Throughout the world, the increased incidences of abiotic and biotic stresses impacting productivity in principal crops are being witnessed. Decline in agricultural productivity is coming into picture due to adverse climatic conditions creating abiotic stresses are among the principal limiting factors (Grayson, 2013) [19]. It has been reported that only 3.5% of the global land area is accounted for not being affected by any environmental constraints. About seventy percent of the reductions in worldwide crop production are caused by abiotic stresses which include drought or soil moisture stress, low/high temperature, soil salinity/alkalinity, low pH, light intensity, submergence, anaerobiosis, nutrient starvation and metal toxicity (Bailey-Serres and Voesenek, 2008) [2]. It has been reported that 64% of the global land area has been affected by water deficit (drought), 13% of the land area by flood (anoxia), salinity 6%, mineral deficiency 9%, acidic soils 15% and cold 57% (Cramer *et al.*, 2011). Around 3.6 billion ha of the world's 5.2 billion ha of dryland agriculture is affected by the problems of erosion, soil degradation and salinity (Riadh *et al.*, 2010) [41]. Due to ever- increasing salinization the area under it almost reached 34 million irrigated hectares and another 16 m ha by water logging (Grover *et al.*, 2011) [21]. Under stress conditions, plant growth is affected by a number of factors such as hormonal and nutritional imbalance, ion toxicity, physiological disorders, susceptibility to diseases, etc. In order to combat adverse environmental situations, plants developed an array of protective mechanisms acquired during the course of evolution. A major challenge is to develop efficient, low cost, easily adaptable methods for the abiotic stress management. Extensive research is being carried out to develop mitigation strategies to cope with abiotic stresses, through development of heat and drought tolerant varieties, shifting the crop calendars, resource management practices, etc. (Venkateswarlu and Shanker, 2009) [53]. While most of these technologies are cost-intensive and time consuming, recent studies indicate that microorganisms can also help crops cope with abiotic stresses. Deleterious harmful effects are exerted by these stressors on crop health as well as cause huge losses to their production. Procurement of management practices ranging from traditional genetics and breeding techniques to present day available novel biotechnological tools are developed by researchers all around the globe to alleviate these stress factors. Use of microorganisms is one such alternative by which abiotic stress can be tackled in an economical, ecofriendly and successful manner.

1. **Mechanisms of bacteria-mediated stress tolerance** Phytohormones play a key role in changing the morphology of roots, providing common adaptation mechanisms to plants when exposed to environmental stresses, such as water and nutrient deficiency, or heavy metal toxicity. Production of auxins, specifically indole acetic acid (IAA) in the plant shoot is transported basipetally to the root tips (Martin & Elliott 1984) [34], where, they enhance cell elongation in low concentrations, resulting in enhanced root growth and also promotes the initiation of lateral roots. Higher concentrations of auxin in the root tips, however, have an inhibitory effect on root growth. Considering the relationship between IAA and the ethylene precursor, 1-aminocyclopropane-1-carboxylic acid (ACC), the inhibition can be either direct or indirect through promoting the synthesis of ethylene. Various researchers have reported that bacteria colonizing the root zone can also influence such modifications in root growth. Promotion of root growth results in a larger root surface, and can, therefore, have positive effects on water acquisition and nutrient uptake. The availability of specific substrates as precursors for phytohormones, such as l-tryptophan for IAA, therefore, is a major factor determining the degree of bacterial stimulation of plant growth. The ACC deaminase activity is another general characteristicamong endophytic and rhizosphere bacteria where they exert beneficial effects on abiotically stressed plants (Saleem *et al.* 2007) [42]. The ACC deaminase positive bacteria can use the immediate ethylene precursor ACC as a source of nitrogen. A decrease in plant ethylene level is caused due to bacterial hydrolysis of ACC which, in turn, results in increased root growth (Glick *et al.*, 1998). However, decreasing the level of ethylene alters the general stress status of the plant, as ethylene plays a key role in stress-related signal transduction pathways. Like ethylene, proline is often synthesized by plants in response to various abiotic stresses, mediating osmotic adjustment, subcellular structure and free radical scavenging stabilization. In abiotically stressed plants, proline synthesis has been shown to be increased in the presence of beneficial bacteria such as *Burkholderia* (Barka *et al.*, 2006) [3]. It has been reported that at the molecular level, gene expression changes related to ethylene production in abiotically stressed plants treated with beneficial bacteria (Timmusk & Wagner, 1999) [49].

Tolerance to drought

Drought is one such abiotic stress which results in devastation of agricultural crops and is estimated to have reduced national cereal production by 9–10% (Lesk *et al.*, 2016) [30]. It is a major factor limiting crop growth and productivity, especially in arid and semi-arid regions. Some microbial species and/or strains that inhabit plant rhizosphere employ different mechanisms to avoid negative effects of drought on plants. The impact of drought can be mitigated through the production of exopolysaccharides, increased circulation of water in the plant, induction of resistance genes, and the synthesis of ACC-deaminase, indole-acetic acid and proline (Grover *et al*., 2010) [22]. Though the effects of drought stress on plant growth are known, the different tolerance mechanisms involved vary from one plant species to another. Plant has the ability to tolerate abiotic stress in association with microbes, such as mycorrhizal fungi, endophytic fungi, rhizobial and plant-growth-promoting rhizobacteria, which play a vital role in modulating their physiological processes. PGPR has proven to mitigate the impact of drought on plants through a process so called induced systemic tolerance (IST) which includes: a) production of cytokinins, b) production of antioxidants and c) degradation of the ethylene precursor ACC by bacterial ACC deaminase. The advantages of using PGPR confer drought tolerance to many plant hosts such as monocotyledonous and dicotyledonous row and vegetable crop species.

Mechanisms to combat/alleviate drought

Rooting characteristics for water uptake

Root system architecture is one of the most important adaptive traits among the many that plants possess to endure drought (Huang *et al.,* 2014) [28]. Under drought conditions, specific root traits associated with maintaining plant productivity include increases in numbers of roots with smaller diameters and a deeper root system (Comas *et al*., 2013) [12]. PGPR treated in plants has been reported to promote root growth and to alter the root architecture (Ngumbi, 2011) [38]. More research is needed to chalk out the correlation between bacterial-mediated improved root architecture and drought tolerance.

Characteristics of shoot growth

Inhibition of shoot growth is one of the key responses to drought stress which benefits plants by limiting the leaf area available for evaporative loss of limited water reserves (Skirycz and Inzé, 2010) [46]. Vardharajula *et al*. (2011) [51] showed that corn plants inoculated with plant growth- promoting *Bacillus* spp. improved shoot growth. The above studies clearly show that increase in shoot growth and improvements in plant growth takes place with the treatment of plants with selected strains of PGPR which help plants tolerate drought stress.

Relative water content

One of the best criteria for measuring plant water status is relative water content (RWC) in plant leaves because it is involved in the metabolic activity in tissues. It has been reported that species that are better adapted to dry environments have high RWC (Jarvis and Jarvis, 1963) [29]. Therefore, an important drought tolerance strategy to be considered is increase in RWC.

Osmotic adjustment for drought tolerance

At the cellular level, osmotic adjustment is one of the key adaptations that help plants tolerate drought-induced damage (Farooq *et al.,* 2009) [14]. One of the most important osmolytes that accumulate in plants experiencing drought stress is proline (Huang *et al.*, 2014) [28]. Previous studies indicate that plants with high levels of proline would be better at combatting drought stress. Apart from acting as an osmolyte for osmotic adjustment, stabilizing sub-cellular structures (e.g. proteins and membranes), scavenging free radicals and buffering cellular redox potential are other key functions of proline (Hayat *et al.*, 2012) [25].

Antioxidant metabolism

Drought stress causes enhanced production of a variety of reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2), singlet oxygen ($1O^2$), superoxide radical (O^{2-}), and the hydroxyl radical (HO^-) (Helena and Carvalho, 2008). To overcome the deleterious effects of ROS, plants are acquainted with enzymatic and non-enzymatic oxidants also known as scavenging enzymes that act in an efficient and cooperative manner. These enzymatic antioxidants include catalase (CAT), superoxide dismutase (SOD), peroxidase (POX), glutathione reductase (GR), and ascorbate peroxidase (APX). Therefore, drought-tolerant plants develop effective ROS scavenging systems (Huang *et al*., 2014) [28]. A significant increase in several scavenging enzymes including APX, SOD, and CAT was reported by Gururani *et al.* (2013) [23]. For example, under drought stress the specific activity of CAT was up to 1.8 times higher in PGPR- treated plants compared with that in non-treated plants. Conferment of drought tolerance is done by treating plants with selected PGPR which induces the over-production of these ROS- scavenging enzymes, which in turn reduces the level of over- produced ROS.

Plant growth substances

Plant growth regulators (substances applied externally) along with several phytohormones, including auxins, gibberellins (GAs), cytokinins (CKs), ethylene (ET), and abscisic acid (ABA) are responsible for plant growth and development including shoot (Farooq *et al.*, 2009) [14]. Promotion of plant growth are by GAs and CKs while ethylene and abscisic acid inhibit growth (Taiz and Zeiger, 2010) [47]. Such modifications include changing the balance of CKs and ABA, decreasing ET production, and/or IAA signaling. Bacterial-mediated drought tolerance is achieved when PGPR are applied in drought stress conditions.

Auxin

An important growth regulator which influences a large number of diverse cellular functions including differentiation of vascular tissues, initiation of lateral and adventitious roots, stimulation of cell division, elongation of stems and roots, and orientation of root and shoot growth in response to light and gravity is auxin, also referred to as indole-3-acetic acid (IAA) (Glick, 1995) [17]. Increased IAA production was observed when clover (*Trifolium repens* L.) plants were treated with PGPR (*P. putida and B. megaterium*) which increased shoot and root biomass and water content under drought stress (Marulanda *et al*., 2009).

Ethylene and ACC deaminase

Several stress signals including mechanical wounding, chemicals and metals, flooding, extreme temperatures, pathogen infection and drought leads to synthesis of ethylene (ET) at higher rates. Some PGPR syntheises the enzyme ACC deaminase that cleaves ACC and reduces ethylene levels in the rhizoplane. The inhibitory effect of higher ET concentrations is eliminated by reduced ACC levels resulting in a reduction in the levels of endogenous ET (Glick *et al*., 1998) [18].

Abscisic acid

Abscisic acid (ABA) plays important roles in many physiological processes in plants and is considered as an important factor for the response to environmental stresses such as drought (Cohen *et al*., 2015) [11]. Similarly, Cohen *et al.* (2008) [9] reported that higher ABA content was observed in arabidopsis plants that were treated with *PGPR Azospirillum brasilense* Sp245 than non-treated plants. To explain the mechanisms by which ABA can enhance drought tolerance, several other explanations have been advanced.

Tolerance to Excessive moisture/ flood

Excessive moisture conditions allow microorganisms to take up the available oxygen eventually accumulating toxic substances in the soil. In such conditions, permeability of roots, water absorption and nutrients uptake is reduced by the plant which thereby, reduces the growth of roots and aboveground plant parts. Excessive moisture provokes roots to release large quantities of aminocyclopropane carboxylate- 1 (ACC) into the soil. Some groups of bacteria secrete the enzyme ACC-deaminase which degrades ACC and thereby, reduces its concentration in the soil. In soils with excessive moisture, bacteria such as *Enterobacter cloacae* and *Pseudomonas putida* predominate over fungi and actinomycetes (Gricho and Glick, 2001) [20]. Mitigation of stress is caused in plants with excessive moisture condition by mycorrhizal fungi (Grover *et al*., 2010) [22]. It is hypothesized that, under conditions of excessive moisture, sensitive plant species are damaged due to the accumulation of acetaldehyde and the high toxicity of ethanol intermediates in roots. The tolerance of *Pterocarpus officinalis* to excessive moisture is increased by *Glomus intraradices* (Grover *et al*., 2010) [22].

Tolerance to extreme temperatures

Most biological reactions are basically temperature dependent. High temperature promotes plant growth and development, while low temperature is the most important limiting factor to the productivity and geographic distribution of agricultural crops. The rate of nutrient decomposition and its release increases with exposure to high temperature. The total number of bacteria and the number of nitrogen-fixing bacteria in soil was unaffected by burning of crop residues in a wheat- soybean rotation (Harris *et al.*, 1995) [24]. One month after burning of vegetation cover, the bacterial population was 25 times lower and the number of fungi decreased by about 5% compared with a soil that was not subjected to burning (Vázquez *et al.*, 1993). Grover *et al.* (2010) [22] reported that some bacterial species and strains affect plant tolerance to high temperature. For example, thermo-tolerance in sorghum seedlings is caused by *Pseudomonas* sp. strain NBRI0987 which consequently synthesizes high molecular weight proteins in leaves thus increasing the plant biomass. The ability of plants to withstand cold can be enhanced upon exposure to low, non-freezing temperatures. When grown on geothermal soil, the endophytic fungus *Cuvularia* sp. which has been isolated from *Dichathelium lanuginosum* is thermo- tolerant to temperatures of 50°C to 65°C (Redman *et al.*, 2002) [40] and when the plant and the fungus was grown separately, they were unable to tolerate temperatures above 38°C. Authors suggested that bacterially mediated tolerance to low temperatures is positively correlated with the induction of ISR.

Tolerance to high salinity

Soil salinity is a serious agriculture problem worldwide, which leads to detrimental effects on plant growth and productivity. Bui (2013) [8] reported that more than 6% of the world's land is affected by salt stress, especially in arid and semi-arid areas. It is expected that by the year 2050, more than 50% of all agricultural soils will be affected by salinity (Ashraf, 1994) [1]. Occurrence of salinity is due to natural or human-induced processes that result in the accumulation of dissolved salts in the soil water to an extent that limits plant growth. Salt stress results in a number of physiological changes like ionic influxes, oxidant imbalances, cell-division impairment, and membrane degeneration in plants. Oxidative stress in plants is produced due to salinity through the production of reactive oxygen species (ROS). Improving salt tolerance of crop plants on saline soil is the need of the hour. Plants can be protected from salt effects by the introduction of plant growth- promoting and salt-tolerant microbes to soil. Microorganisms use different mechanisms to combat the salinity stress in agricultural crops. A lot of work has been done on plant growth- promoting rhizobacteria (PGPR) for improving crop performance under adverse saline conditions (Bashan *et al.*, 2014) [4]. During salt stress, seedling development can be supported by the exopolysaccharides secreted by bacteria as well as nitrogen-fixing bacteria (Wu *et al*., 2012) [55]. Moreover, bacteria producing GA and IAA promote seed germination and plant growth against salt stress. The xylem flow of K^+ increases from root to shoot by bacteria which maintains sufficient levels of K^+ to alleviate the Na^+ toxicity (Wang *et al*., 2016) [64]. Growth and development of tomatoes, peppers, beans, and lettuce grown in saline environments is affected by some rhizobacterial strains (PGPR) (Grover *et al*., 2010) [22]. Under conditions of stress caused by high salinity, wheat seedlings inoculated with bacteria produces exopolysaccharates (EPS) which affect the restriction of sodium uptake and stimulation of plant growth (Grover *et al.*, 2010) [22]. A mechanism of salt tolerance by producing exopolysaccharides (EPS) imposed by *Pseudomonas* sp. PMDzncd2003 on rice germination under salinity stress showed better root colonizing capability of *Pseudomonas* sp. leading to enhanced tolerance toward salinity (Sen and Chandrasekhar, 2014) [44].

Tolerance to Metal toxicity

Heavy metals are elements comprising of transition metals, some metalloids, lanthanides and actinides with a density higher than 5 g cm^{-3} (Schützendübel and Polle, 2002) [43]. In most plants, the typical concentrations ($\mu g\ g^{-1)}$ of heavy metals are 50 for Zn, 10 for Cu, 200 for Mn, 0.05 for Cd, 0.1 for As, 1 for Pb and 1.5 for Ni (van der Ent *et al.*, 2013). Among heavy metals, some elements such as Zn, Cu and Mn, are required as micronutrients, but higher concentrations affect negatively plant metabolism and functioning by being toxic (Ferraz *et al*., 2012) [15]. Other heavy metals such as Cd, As, Pb, Hg and Ni, are non-nutritional and toxic elements for most organisms (He *et al.*, 2013) [32]. The negative impact of heavy metals on plants is indirectly reduced by microorganisms by binding soluble heavy metals in three ways (biosorption, bioaccumulation, and the binding by metabolic products. A possible way to remove different metal from the soil is to use metal accumulating plants for the removal of metals from contaminated soil. Ectomycorrhizas (EMs) are mutualistic associations between certain soil fungi and higher plants. Various researches have been done in the field of mycorrhiza-modulated host plant tolerance to heavy metals (Rajkumar *et al*., 2012) [39]. Thereby, plants with the help of EMF and other microbes can be used for bioremediation of heavy metal polluted soils (Rajkumar *et al.*, 2012) [39]. EMs has the ability to modulate the cellular, physiological and molecular processes of host plants, resulting in altered responses of the colonized plants to heavy metals.

Mechanisms of EM-modulated host plant tolerance to heavy metals

Cellular mechanisms

In the desirable concentrations range, the nutritional heavy metals Zn, Cu and Mn are beneficial to ectomycorrhizal fungi and host plants. For instance, under normal conditions, Zn is translocated to the cytosol, chloroplasts, mitochondria and peroxisomes (Broadley *et al.*, 2007) [7]. At higher concentrations, toxicity of these metals is altered by ectomycorrhizal plants. Certain cellular mechanisms are involved in detoxification of excess heavy metals such as (i) the biofilter function of ectomycorrhizal fungi and (ii) subcellular sequestration of these metals in ectomycorrhizal plants (Colpaert *et al*., 2011) [11]. Protective mechanisms are employed by ectomycorrhizal fungi similar to those of their host plants (Colpaert *et al.*, 2011) [11] including binding to cell walls and sequestration in the vacuole. Further protective measures are: (i) binding of heavy metals to extracellular exudates, (ii) decreased uptake and/or pumping metal ions out of cytosol via transporters located at the plasma membrane,
(iii) chelation of metal ions in cytosol by com-pounds, such as glutathione, phytochelatins and metallothioneins, (iv) compartmentation of metals in other subcellular structures to avoid accumulation of metal ions in cytosol, and (v) repair of metal damaged biomolecules (Colpaert *et al.*, 2011) [11]. The two main cellular mechanisms for Cd detoxification of fungus
P. involutus were binding of Cd to the cell wall and accumulation of Cd in vacuole (Blaudez *et al.*, 2000) [6].

Physiological mechanisms

Numerous physiological changes occur in roots and even at the whole-plant level of the host during the establishment and functioning of EMs (Li *et al*., 2012) [26]. These physiological responses comprises of altered uptake of nutrients, particularly of phosphorus, changed photosynthetic rates and photosynthate supply to roots, improved water status and increased osmolality, varied concentrations of free amino acids, phytohormones and fatty acids, and shifts in the ROS balance (Beniwal *et al*., 2010; Schützendübel and Polle, 2002) [5, 43]. For instance, *P. involutus* inoculated in *P.* × *canescens*, resulted in elevated phosphorus concentrations in roots and leaves (Luo *et al.*, 2011) [8], and increased net influxes of Ca^{2+} and K^+ into the roots (Li *et al*., 2012) [26]. For the non- nutritional toxic heavy metals, i.e., Cd, Pb, Hg, Ni and As, EM-induced physiological changes in host plants is due to modified tolerance of ectomycorrhizal plants to these metals.

Molecular mechanisms

Successful defense of heavy metal toxicity requires coordinated activation of detoxification processes. An important benefit provided by EMF is priming of these pathways in the host plants. Several molecular pathways are employed by ectomycorrhizal plants to regulate the interaction between host plants and heavy metals: (i) EMs can modify the activities of transporters for metal uptake and transport at the transcript and protein levels (Ma *et al.*, 2013) [32], (ii) EMs can modulate the availability of chelating molecules for binding heavy metals in cells (Ma *et al.*, 2013; Seth *et al*., 2012) [32, 45],

(iii) EMs can alter the transcriptomes of host plants to mediate defense against stresses including heavy metals (Flores- Monterroso *et al*., 2013) [16]. A ZIP family transporter, NcZNT1 *in N. caerulescens*, is a plasma membrane-localized transporter for Zn uptake that is regulated at the transcript and protein levels (Milner *et al*., 2012) [37]. Under Ni-stress, transcriptome analysis revealed Ni-induced genes encoding proteins putatively involved in the modification of cellular components and molecular functions in *P. albus* (Majorel *et al.*, 2012) [33]. Most studies to date have addressed transport processes only in the plants and not in the associations between EMF and their hosts but initial evidence showed that metal trafficking is affected by ectomycorrhizal fungi, thereby affecting plant performance.

To ameliorate heavy metal polluted soils, heavy metal tolerant ectomycorrhizal fungal isolates, PGPR and AMF may be employed for bioremediation as an environmentally friendly technology. In the last decades, progress has been made in the identification of heavy metal tolerant species/isolates of ectomycorrhizal fungi and plants.

Tolerance to nutrient deficiency

Phosphorus, potassium, iron, zinc and copper, are such nutrient elements which possess limited mobility in the soil. In the case of phosphorus, plant exudates such as phosphatases and organic acids mobilize its insoluble form in the soil. Exuded carbohydrates serve as a carbon source for P-solubilizing microorganism also indirectly contribute to phosphorus mobilization. This led to the speculation that higher amounts of plant carbohydrate exudates can be provoked by bacterially produced IAA and therefore, result in a better nutrient status of the bacteria. In turn, the bacteria are able to mobilize more P; thus, under P-deficient conditions, plant growth-promoting effects of P-solubilizing bacteria would be more pronounced. As such, bacterial survival ensures their contribution to the amelioration of abiotic stress, and hence, to plant growth promotion. Accumulating evidence suggests that the ability to adapt to adverse environmental conditions and in particular to abiotic stress factors, mineral nutritional status of plants is affected greatly.

Conclusion and future aspects

Microorganisms play an important role to help agricultural plants to increase their tolerance and adaptation to abiotic stresses. The complex and dynamic interactions between microorganisms and plant roots under conditions of abiotic stress affect the plants as well as the physical, chemical, and structural properties of soil. Some microbial species and strains could play an important role for understanding plant tolerance to stress, adaptation to stress, and mechanisms that develop in plants under stress conditions. The interaction of microbes with plants is a dynamic, sophisticated phenomenon wherein several external factors affect the structure and species composition of the bacterial communities. An understanding of microbial composition that is associated with plants is fundamental to understanding how plants' biological processes are influenced by environmental factors. Certain strains of PGPR, AM, EM can help plants tolerate drought stress. Some of the physiological mechanisms that have been proposed include alterations in root architecture which results in improved water and nutrient uptake, with positive effects on the overall plant growth, increase in relative water content, increase in several organic and inorganic solutes as well as an increase in the synthesis of osmolytes including proline, increase in antioxidant enzymes that scavenge for reactive oxygen species, and manipulation of phytohormones including IAA, ABA, and CK. Although it is clear that various PGPR strains help plants mitigate drought stress, the mechanisms involved remain largely speculative. Studies also suggests that bacterial collections from drought-prone areas performed better in increasing plants' tolerance to drought stress than those that were isolated from areas that do not experience drought. Techniques to exploit transcriptomics, proteomics and metabolics of plant-microbe interactions *in- situ* in soil should be developed. Application of multi strain bacterial inoculation ("cocktails") could be another effective approach. Numerous studies are going on regarding Induced Systemic Tolerance (IST) by Plant growth promoting bacteria but IST by other soil microorganisms remain still elusive. Further research is needed to elucidate the molecular and physiological mechanisms of plant-bacterial interactions to promote different abiotic stress tolerance in plants.

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