Pragmatic role of microbial plant biostimulants in abiotic stress relief in crop plants

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Introduction

Plants are sessile in nature and are continuously exposed to various environmental stresses, including extreme temperatures, high salinity, heavy metals, waterlogging, drought, ultraviolet radiation, and limited soil nutrient availability. These factors hinder plant growth and development, disturb the soil ecosystem, and can result in significant losses to crop productivity (He et al. 2018, Bera et al. 2022, Moon and Ali 2022a). It is estimated that approximately 90% of global arable land is prone to one or more environmental stresses, resulting in 70% yield losses in major crops (Waqas et al. 2019). Suzuki et al. (2014) reported that heat and drought stress caused $200 billion losses in the USA between 1980 and 2012. Abiotic stresses have a significant impact on plant developmental cascades through physiological functions and biochemical processes that modulate molecular mechanisms that are directly associated with the growth and productivity of plants (Tandzi et al. 2018, Moon and Ali 2022a). The negative effects of abiotic stresses (salinity, drought, extreme temperature, waterlogging, and heavy metals) on the growth, development, and yield of crops and other plants are listed in Table 1. Millions of microorganisms (fungi, bacteria, viruses, archaea, and protozoa) live in the soil microbiome, and the interaction between microbes and plants is critical for sustainable agriculture. However, abiotic stresses greatly affect microbial diversity in the soil, shaping the rhizospheric microbial flora and directly influencing plant functional traits.

Various strategies have been employed to alleviate the adverse effects of abiotic stresses and to enhance the growth and productivity of crop plants. These strategies include modern farming techniques and irrigation systems, use of different chemicals, and development of genetically modified crops (Ali and Kim 2019, Moon and Ali 2022a, Moon and Ali 2022b). These methodologies have contributed substantially to the modern agricultural system and crop production. However, they have also exerted adverse effects on the natural ecosystem. Generally, most chemicals and fertilizers are wasted in the fields and/or kill beneficial microorganisms. It has been estimated that a very small amount (approximately 0.1%) of insecticides and pesticides impact the targeted organisms, and the remaining contaminate the immediate environment (Gill and Garg 2014) mainly due to the overuse of chemical-based products on crops. Recently, a variety of plant biostimulants (substances/microorganisms) have been used to augment nutrition efficiency, enhance abiotic stress tolerance, augment the growth of beneficial microorganisms, and increase crop productivity (Ruzzi and Aroca 2015a, Colla et al. 2017, Luziati et al. 2019).

The term ‘Plant Biostimulant’ is also considered for commercial products which contain a mixture of substances or microorganisms used for the improvement of nutritional effectiveness in plants, and alleviation of abiotic stress damages. The international biostimulant market is expected to grow rapidly at an annual growth rate of 10.2% between 2017–2025. In contrast, microbial-based plant biostimulants account for less than 25% of the available commercial biosimilar products in the global market (Bulgari et al. 2019, Hamid et al. 2021). Microbial plant biostimulants (MPBs) are applied to crops to enhance the acquisition of different nutrients and their utilization by plants, improving the growth and productivity of the plant. MPBs may include plant growth-promoting rhizobacteria (PGPR), mycorrhizal and non-mycorrhizal fungi, and bacterial endosymbionts, all of which utilize direct and indirect mechanisms to promote plant growth and development under normal and stressful conditions. MPBs establish and maintain sufficient activity in the vicinity of plants and modulate plant responses to various stresses (Du Jardin 2015, Ali et al. 2017).
The use of MPBs is a cost-effective and environmentally beneficial strategy as they augment plant immune systems, assimilate nutrients, and help crops tolerate abiotic stresses (Nepali et al. 2020). Microbes such as *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Pseudomonas*, and arbuscular mycorrhizal fungi (AMF) act as MPBs and have been reported to enhance plant growth and mitigate abiotic stresses in crops such as tomato, potato, cabbage, broccoli, maize, and rice (Asaf et al. 2018, Kim et al. 2020, Li et al. 2020, Kubi et al. 2021). MPBs support plant nutrition and induce significant changes in secondary metabolism and tolerance to soil and environmental stresses (Rouphael and Colla 2020). They also develop different mechanisms and strategies to maintain plant health under adverse conditions, including alteration of the composition of the cell wall and high solute accumulation, which allows enhanced water retention and increased tolerance to ionic and osmotic stresses (Van Oosten et al. 2017). The ability of MPBs to protect plants from environmental stresses is critical for crop survival (Nepali et al. 2020), and the application of MPBs is a desirable, pragmatic, and environmentally friendly approach to mitigate the adverse effects of various stresses.

Colla and Rouphael (2015) proposed three main categories of MPBs (AMF, PGPR, and *Trichoderma* spp.). They also critically examined the admission process for MPBs under the Fertilizing Product Regulation (EU) 2019/1009) on May 17, 2021. A fraction of the microorganisms listed in the component material category (CMC) 7 (*Azotobacter* spp., *Rhizobium* spp., *Mycorrhizal* fungi, and *Azospirillum* spp.) have now been accepted as MPBs. The regulatory procedure for adding microbes to the approved list in CMC 7 and the application procedure for the microbes need to be elucidated. The Farm Bill (2018) was passed into a law under the Agricultural Improvement Act (AIA-2018) and had basic recommendations regarding plant biostimulants. Following the Farm Bill (2018), the Environmental Protection Agency (EPA) of the United States of America (USA) released draft guidance on plant biostimulants in March 2019 (Madende and Hayes 2020). Similar to Europe, the regulation of MPBs in the USA, Russia, India, and many other countries is still not clearly defined, which is expected to slow its expected global market growth. On the other hand, China has completed a series of amendments and formed a basic regulatory system to manage product specification, labeling, safety and efficacy evaluation by the end of 2017. However, legislative procedures for MPBs need to be harmonized at a global level. The present mini-review discusses the role of MPBs as a biological tool for the alleviation of different abiotic stresses, reports on the current knowledge on the use of MPBs, and discusses the diversity and characteristics of MPBs in abiotic stress relief in crops.

### Prolific role of MPBs under abiotic stress

Plant growth and development are supported by MPBs both directly and indirectly (Figure 1). At different phases of plant development and under different environmental conditions, these processes may be simultaneously or sequentially active. Some prominent examples of direct mechanisms include: (i) production of phytohormones such as indole acetic acid (IAA), abscisic acid (ABA), gibberellic acids (GAs), and cytokinins, (ii) biological nitrogen fixation, and (iii) increased mineral nutrient solubilization. Indirect mechanisms include: (i) production of 1-aminoacyclopropene-1-carboxylic acid (ACC) deaminase, (ii) siderophore production, (iii) antioxidant enzyme production, (iv) production of antibacterial and antifungal compounds, and (v) production of exopolysaccharides (EPS) and biofilm formation. The identification and application of MPBs may represent an important biotechnological approach for mitigating the adverse effects of abiotic stresses on crops under different environmental conditions.

MPBs primarily modulate plant hormone status by secreting exogenous hormones and bioactive secondary metabolites that contribute substantially to abiotic stress relief. Auxin is the major plant hormone produced by MPBs and its biosynthesis occurs via multiple pathways in various microbes. IAA produced by MPBs is a well-studied bacterial and fungal signaling molecule involved in plant-microbe interactions. The IAA producing MPB *Azospirillum brasilense* improves root development in wheat (Dobbelare et al. 1999, Saepeen et al. 2008). Similarly, GA is another important class of plant hormones that plays an important

| Abiotic Stress | Effects on Plants |
|---------------|-------------------|
| Salt stress   | Higher concentration of osmolytes, Lower osmotic potential, Decrease water contents, Inhibition of photosynthesis, Stomatal closure, Poor root growth, Stunted plant growth, Chlorosis, Leaf rolling, Altered metabolism, High sodium transport to shoot, Oxidative stress, Lower uptake of K, Zn, and P, Less biomass and grain yield. |
| Drought stress| Reduce stomatal conductance, Reduce leaf internal CO₂, Increase osmotic pressure, Reduction in N assimilation, Altered respiration/transpiration rate, Altered Photosynthetic activity, Decrease chlorophyll content, Increase ABA synthesis, Uprogulation of antioxidants, Reduced ROS accumulation, Expression of stress responsive genes, Reduce leaf area and plant height, Increase dry matter in root and shoot, Early senescence, Reduction in biomass and productivity. |
| High Temperature stress | Osmoprotectant accumulation, Activation of antioxidant system, Decrease chlorophyll content, Decreased respiration, Adjustment in electron transport capacity, Expression of chaperons and heat shock proteins, Stomatal closure, Change in leaf orientation, Leaf abscission and senescence, Increased stability of thylakoid membrane, Reduction in biomass and yield. |
| Low Temperature stress | Enhanced production of antioxidants, Reduced cell size, Increased stomatal densities, Greater xylem vessels, Induced retention of H₂O in plants, Changes in membrane structure, Less biomass and grain production, Protoplasmic streaming and electrolyte leakage, Surface lesions on fruits and leaves, Decrease chlorophyll content, Vascular browning or Internal discoloration. |
| Heavy Metal stress | Reduce biomass and grain production, Reduced cell size and protein biosynthesis, Decrease respiration and water status, Decrease photosynthesis and chlorophyll content, Increased electrolyte leakage, Slowdown mineral uptake and Seed germination, Enhanced production of antioxidants, Increased stomatal densities, Damage to DNA, Chromosomal aberrations and abnormal mitosis and meiosis. |
| Waterlogging stress | Reduction in yield, Reduction in leaf area index and chlorosis, Decrease water uptake, Decrease chlorophyll content, Damage to photosystem II, Reduction in photosynthesis, Increased transpiration, Increased stomatal densities, Reduce nutrients uptake, decrease protein contents, Accumulation of alcohol dehydrogenase, Production of ROS, Stress ethylene production, Reduced gibberellins, increased ABA and reduce cytokinins level. |
role in the regulation of cell division and elongation as well as meristematic activity in the roots and leaves. Several GA-producing MPBs enhance plant growth and tolerance to abiotic stresses such as heat, salinity, heavy metals, and drought (Choi et al. 2005, Kang et al., 2015, Backer et al. 2018).

Phosphorus is an essential macronutrient that plays a vital role in the metabolic and physiological processes of crop plants under normal and stressful conditions. The ability of MPBs to solubilize insoluble phosphate by releasing organic acids increases the accessibility of these essential elements to crops, thereby improving soil fertility, crop productivity, and tolerance under abiotic stress conditions. MPBs such as *Pseudomonas mendocina* and an AMF (*Glomus intraradices*) significantly enhance root phosphatase activity, accumulation of proline, and antioxidants in lettuce leaves under drought stress (Kohler et al. 2008). Similarly, plants produce an increased amount of ACC synthase under abiotic stress conditions, which converts S-adenosyl-l-methionine (SAM) into ACC in greater amounts, and an increased amount of ethylene is produced with the oxidation of ACC by ACC oxidase. The production of ethylene leads to physiological and anatomical damage to plants under abiotic stress conditions. MPBs that produce ACC deaminase reduce the ACC content by hydrolyzing exuded ACC and lowering the level of stress ethylene in host plant tissues. In a recent study, Kumawat et al. (2021) reported the coordinated effect of two compatible non-pathogenic *Rhizobium* spp. LSMR-32 and *Enterococcus mundtii* LSMRS-3 are salt stress-tolerant and produce ACC deaminase. They concluded that the co-inoculation of both strains significantly improved the grain yield (8.92%) of spring mungbeans and alleviated the adverse effects of salinity stress. Similarly, ACC deaminase enzyme activity and IAA production by different microbial isolates are considered the most important plant growth-promoting traits, and a number of different rhizobacteria have been evaluated and added to the consortium of biofertilizers and MPBs.

MPBs that produce siderophores may be a promising alternative to chemical fertilizers as they address abiotic stress while also increasing the available iron transport, modulating Na/H antiporters, and different ion channels. Similarly, several MPBs produce EPS, which is responsible for attachment to soil particles, root surfaces, and other microorganisms, and plays an important role in plant growth by stabilizing soil structure, boosting water potential, and cation exchange capacity (Upadhyay et al. 2011). EPS usually form an enclosed matrix of microcolonies that confers protection against environmental floatation, water, nutrient retention, and epiphytic colonization (Balsanelli et al. 2014). MPBs improve soil structure by increasing the volume of rhizospheric soil macropores, improving water potential, and enhancing the uptake of nutrients by plants (Naseem and Bano, 2014). *Pseudomonas mendocina*, an EPS-producing MPB, was inoculated with *Arbuscular Mycorrhizal Glomus* to stabilize soil aggregation in lettuce in the field (Kohler et al., 2006). Moreover, halotolerant MPBs that produce EPS can also store Na ions absorbed by plants, mitigating the impact of salt stress. Similarly, MPBs (YNA59) produce EPS and induce drought stress tolerance in broccoli (Kim et al. 2020).

The exogenous application of polyamines increases abiotic stress tolerance in various plants (Gupta et al. 2013). However, the secretion and function of polyamines produced by MPBs are largely unexplored. Microbes such as *Bacillus megaterium* secrete polyamines and increase cellular polyamines in *Arabidopsis* via polyamine-mediated pathways. Inoculation with microbial biostimulants results in greater biomass, elevated photosynthetic capacity, and higher antioxidant enzyme activity (Zhou et al. 2016). Similarly, low-molecular-weight volatile organic compounds (VOCs) produced by MPBs have been shown to induce a variety of physiological changes in plants, promote growth and development, and greatly modulate stress responses under different environmental stresses (Ilangumaran and...
MPBs induce abiotic stress tolerance in crop plants

Applying MPBs effectively improves abiotic stress tolerance in plants. MPBs enhance abiotic stress tolerance through various mechanisms, as explained in detail above. A few recent studies on plant growth-promoting MPBs that can be employed to promote plant growth and mitigate abiotic stress in various crop plants are listed in Table 2.

Role of MPBs in salinity stress tolerance

Soil salinization accounts for more than 6% of global land, rendering 22%–33% of the total cultivated and irrigated agrarian land with reduced crop productivity (Khan et al. 2019, Hamayun et al. 2021). By 2050, approximately 50% of arable land will be threatened by soil salinity (Sahile et al. 2021). Several plant growth-promoting MPBs have been reported to induce salinity stress tolerance in various crops. Plant growth-promoting MPBs alleviate salinity stress through various synergistic mechanisms, including osmotic regulation, increased nutrient uptake, phytohormone signaling, and photosynthesis amelioration. Furthermore, MPBs decrease Na uptake, enhance N, P, and K uptake, increase chlorophyll content, activate different antioxidants, and regulate hormonal regulation under salinity stress (Alexander et al. 2020, Mellidou et al. 2021, Gul et al. 2022, Sapre et al. 2022). Miceli et al. (2021) reported that the application of MPB enhanced salt-tolerance in Solanum lycopersicum and lettuce plants. Before seeding, the seeds were treated with two different commercial MPBs, TNC Bactorex® (containing Bacillus spp.) and Florisol Micorrize (containing Agrobacterium radiobacter, Streptomyces sp., and Bacillus subtilis). Seedling sensitivity to salt stress was modulated when MPBs were used to enhance plant growth-promoting attributes, such as biomass (fresh and dry), leaf number, and area of unstressed seedlings.

Similarly, MPBs contributed substantially to salt stress tolerance when treated with Florisol Micorrize. Inoculating MPBs could be a pragmatic solution for improving the growth of lettuce and Solanum lycopersicum and reducing the detrimental effects of water with high salt content in vegetable nurseries and field conditions. Likewise, Gururanil et al. (2013) applied two Bacillus isolates to S. tuberosum plants and reported a significant tolerance to abiotic stresses such as salinity, drought, and heavy metals, improving plant height, tuber size, leaf number, and productivity. Previous studies have indicated that all analyzed MPBs showed beneficial effects on both productive and qualitative parameters of crops under abiotic stress conditions.

Role of MPBs in drought stress tolerance

Similarly, water use efficiency and drought stress tolerance can be improved by inoculating plants with different MPBs. According to Batool et al. (2020) and Begum et al. (2022), MPB application is a sustainable approach for promoting crop growth and tolerance towards water-deficient conditions. MPBs enhance drought stress tolerance by releasing different phytohormones, volatile organic compounds, a variety of exopolysaccharides, and ACC deaminase, thereby modulating osmolytes, expressing stress-responsive genes, and aggravating modifications in root structure (Barnawal et al. 2017, Niu et al. 2018, Moon and Ali 2022a). Mannino et al. (2020) investigated the effect of microbial inocula on S. lycopersicum (cv. San Marzano) resistance to drought stress conditions. A mixture of different microbial inocula (such as a single AMF species, a combination of three AMF species, a combination of two PGPB, and a commercial inoculum) was used to inoculate the tomato plants to verify their effects on drought stress tolerance by evaluating biochemical stress markers and hormonal profiles. They concluded that responses of the tomato plant to drought vary depending on the microbial inocula, highlighting the need to determine the best plant/microorganism genotype combination(s) to maximize plant performance and tolerance under such stressful conditions.

Additionally, Efthimiadou et al. (2020) studied the effect of MPBs such as Azotobacter chroococcum, Bacillus subtilis, Bacillus megatherium, and their combinations using soil and foliar application methods on maize under Mediterranean conditions (hot, dry summer, and cool, wet winters). Treatment with A. chroococcum increased the photosynthetic rate, chlorophyll content, and transpiration rate. In the soil zone application, plants treated with B. megatherium and the mixture (1:1) of A. chroococcum and B. subtilis produced the best maize yields. Owing to the high demand for a sustainable agricultural production system that will protect soil fertility, MPBs are cutting-edge technologies that can boost agricultural output while reducing the negative effects of environmental fluctuations (Castiglione et al. 2021). MPBs have been shown to improve abiotic stress tolerance in various crops. However, little is known about the biochemical and physiological alterations associated with MPB priming in stress management.

Role of MPBs in temperature stress tolerance

Thermotolerant MPBs help mitigate heat stress via secretion of several polysaccharides, biofilm formation on root nodules, and enhanced water retention capability. Furthermore, they produce lipopolysaccharides, EPS, and specific heat shock proteins that can actively prevent the detrimental effects of heat stress in plants (Abdelrahman et al. 2018, Ali et al. 2019, Kang et al. 2019). El-Daim et al. (2019) revealed significant metabolic and molecular alterations associated with the ability of Bacillus velezensis to mediate abiotic stress tolerance in wheat. Heat, cold, and drought stresses were applied to the seedlings treated with Bacillus. In all stress settings, Bacillus improved wheat chlorophyll content and survival rate under abiotic stress conditions. They concluded that metabolite analysis with NMR and ESI-MS showed evidence of metabolic reprogramming in Bacillus-treated seedlings, as well as the accumulation of several typical stress metabolites in stressed conditions.
Table 2. Summary of recent researches on microbial biostimulants under abiotic stress.

| Microorganism                        | Plant used                        | Objectives, Results and Conclusion                                                                 | Reference |
|--------------------------------------|-----------------------------------|-----------------------------------------------------------------------------------------------------|-----------|
| **Salinity stress**                  |                                   |                                                                                                     |           |
| *Acinetobacter bereziniae* IG2, Entero bacter ludwigii IG10, Alcaligenes faecalis IG27 | *Pisum sativum*                   | **Objectives:** To investigate the effect of selected PGPR on pea plants under salt stress          | Sapre et al. (2022) |
|                                       |                                   | **Results:** Plants treated with selected microbes revealed lower levels of electrolyte leakage and H2O2 contents under saline conditions compare to untreated plants. Additionally, PGPR improved chlorophyll and proline content, and total soluble sugar. Moreover, in field trials pea plants treated with microbes showed increased growth and yield under 100mM NaCl stress. |           |
|                                       |                                   | **Conclusion:** The PGPRs mitigate the adverse effects of salt stress and promote the growth of the plants |           |
| *Pseudomonas oryzihabitans AXSa06*   | *Solanum lycopersicum*            | **Objectives:** To evaluate the role of *P. oryzihabitans* on tomato seedlings under NaCl stress      | Mellidou et al. (2021) |
|                                       |                                   | **Results:** *P. oryzihabitans AXSa06* aided plant growth and photosynthetic characteristics substantially. Efficiently activated antioxidant metabolism and the primed state of AXSa06 inoculated plants supported by leaf lipid peroxidation and ascorbate contents. Identified signatory molecules of AXSa06 mediated salinity tolerance include amino acids (serine, threonine, glutamate) as well as genes involved in ethylene or abscisic acid. |           |
|                                       |                                   | **Conclusion:** These findings point to a viable long-term option for increasing agricultural yield under salinity stress. |           |
| *Stenotrophomonas maltophilia* BJ01  | *Arachis hypogaea*                | **Objectives:** To evaluate the potential of halotolerant *S. maltophilia* BJ01 on peanut plants under salinity | Alexander et al. (2020) |
|                                       |                                   | **Results:** The interaction of *S. maltophilia* BJ01 supported the growth and development of peanut plants and lower the levels of electrolyte leakage, lipid peroxidation, proline contents and H2O2 contents. Similarly, auxin and total amino acids were enhanced in the plants treated with *S. maltophilia* BJ01. |           |
|                                       |                                   | **Conclusion:** Under salinity stress, the bacterium *S. maltophilia* BJ01 could be used as an effective PGPR for legumes like peanuts. |           |
| *Aneurinibacillus aneurinilyticus* ACCo2, *Paenibacillus sp., ACCo6* | *Phaseolus vulgaris*               | **Objectives:** To isolate ACC deaminase-producing PGPRs and test their effects on salinity-stressed French beans | Gupta and Pandey (2019) |
|                                       |                                   | **Results:** The consortia effects of PGPR alleviated the negative effects of salinity stress and enhanced root length (110%), root fresh weight (45%), shoot length (60%), shoot fresh weight (255%), root biomass (220%) shoot biomass (425%) and total chlorophyll contents (57%) of the seedling treated with ACC02 and ACCo6. |           |
|                                       |                                   | **Conclusion:** *Paenibacillus sp., ACCo6,* and *Aneurinibacillus aneurinilyticus ACC02* facilitate a variety of plant growth promoting activities and improve plant growth in saline conditions. |           |
| *Arthrobacter woluwensis* (AK1), *Microbacterium oxydans* (AK2), *A. aureus* (AK3), *Bacillus megaterium* (AK4), *B. aryabhattai* (AK5) | *Glycine max*                     | **Objectives:** To reduce the negative effects of salinity on soybeans by using halotolerant PGPR.       | Khan et al. (2019b) |
|                                       |                                   | **Results:** The application of selected strain under salinity stress enhanced antioxidant (SOD and GSH) levels and also K+ uptake. While reduced Na+ ion concentration and increased chlorophyll content. Salt tolerant gene GmST1 was highly expressed in AK1 treated plants. While the expression of IAA regulating gene GmLAX3 was depleted in salt stressed plants by 38.92% and upregulated from 11.26% to 43.13% upon treatments of PGPR. |           |
|                                       |                                   | **Conclusion:** The halotolerant PGPR can be applied as a potential biofertilizer, and through controlling phytohormones and gene expression, these biostimulants can help plants cope with salinity stress. |           |
| *Pseudomonas fluorescens* YsS6, *Pseudomonas migulae* BR6 | *Solanum lycopersicum*            | **Objectives:** To evaluate how PGPB with ACC deaminase effect plant growth and development in stressful conditions | Ali et al. (2014) |
|                                       |                                   | **Results:** Plants pretreated with ACC deaminase producing bacteria promoted tomato plant growth significantly even in the absence of salinity stress. The treated plants revealed higher biomass and chlorophyll contents and greater number of flowers and buds compare to other treatments. |           |
|                                       |                                   | **Conclusion:** *P. migulae* BR6 showed better results compare to *P. fluorescens* YsS6 under salinity stress |           |
| *Trichoderma reesi*                   | *Triticum aestivum*               | **Objective:** To mitigate salinity stress by using salt tolerant endophyte.                        | Ikram et al. (2019) |
|                                       |                                   | **Results:** In fungal inoculated wheat plant an increase in plant biomass, growth, chlorophyll content, carotenoids under salinity stress. moreover an increase in mineral uptake (Cao and K) while decrease in Na and stress hormone ABA content in fungal inoculated wheat plants compared with control. |           |
|                                       |                                   | **Conclusion:** Phytohormones producing *T. reesi* improve wheat growth under salinity stress.          |           |
| Microorganism                  | Plant used        | Objectives, Results and Conclusion                                                                 | Reference        |
|-------------------------------|-------------------|---------------------------------------------------------------------------------------------------------------------------------|------------------|
| **Trichoderma longibrachiatum T6** | *Triticum aestivum* | **Objective:** To investigate the role of *T. longibrachiatum T6* under salinity stress. **Results:** Wheat seedling inoculated with isolate T6 showed increase in shoot/root length/biomass under 150mM NaCl stress. Furthermore increase in relative water content, chlorophyll content and antioxidant defence system (SOD, POD, CAT) under salinity stress in F6 inoculated wheat plants. **Conclusion:** Plant growth-promoting *T. longibrachiatum* has a significant effect on alleviating the negative effects of salt stress on wheat seedlings by enhancing antioxidant defenses | Zhang et al. (2016) |
| Mycorrhizal fungi             | Eucalyptus        | **Objective:** To find out the role of arbuscular mycorrhizal fungi in mitigating soil salinity. **Results:** Three salt tolerant AMF species (*Glomus* sp.2, *Gigaspora albida*, *G. decipiens*) were inoculated to eucalyptus seedling under salinity stress. Results showed salinity stress reduce plant performance and eucalypt K/Na ration by increasing chlorophyll and decrease proline content in inoculated plants. **Conclusion:** AMF alleviate the negative impact of salinity on *eucalyptus* physiological and biochemical parameter       | Klimsukon et al., (2021) |
| **Porostereum spadiceum AGH786** | *Glycine max* | **Objective:** To evaluate the combine application of trehalose and LK11 on soybean under natural and PEG stress. **Results:** Soybean plants inoculated with LK11 increase plant growth attributes, amino acid and sugar content under varying PEG stress. Furthermore a significant decrease in ABA and JA were observed in LK11 treated plants. Isolate LK11 and trehalose application increase mRNA gene expression (DREB, MYB) as compared to control. **Conclusion:** Combined application of LK11 and trehalose mitigate the negative effect of drought stress on soybean | Hamayun et al., (2017) |
| **Drought stress**            |                   |                                                                                                                                  |                  |
| **Sphingomonas sp. LK11**     | *Glycine max*     | **Objectives:** To evaluate the combine application of trehalose and LK11 on soybean under natural and PEG stress. **Results:** Soybean plants inoculated with LK11 increase plant growth attributes, amino acid and sugar content under varying PEG stress. Furthermore a significant decrease in ABA and JA were observed in LK11 treated plants. Isolate LK11 and trehalose application increase mRNA gene expression (DREB, MYB) as compared to control. **Conclusion:** Combined application of LK11 and trehalose mitigate the negative effect of drought stress on soybean | Asaf et al. (2018) |
| **Variovorax sp YNA59**       | *Brassica oleracea* | **Objective:** To investigate the role of drought tolerant bacteria on crops under drought stress. **Results:** Isolate Variovorax YNA59 have the ability of producing ABA, sugar production and tolerate oxidative stress like H2O2, SOD, CAT and APX activities in culture broth. Under drought stress isolate YNA59 significantly enhance broccoli growth attributes by decreasing ABA and JA content while increase SA content. Furthermore higher level of SOD, Cat and APX were observed while decrease in GPX in YNA59 treated plants under drought stress. **Conclusion:** Drought tolerant *Variovorax YNA59* have the capability of different PGP traits and upon inoculation to broccoli plants increase different growth parameters by mitigating the negative effect of drought stress. | Kim et al. (2020) |
| **Bacillus subtilis (LDR2)**  | *Triticum aestivum* | **Objectives:** To evaluate phytohormonal and physiological responses of *Bacillus subtilis* (LDR2) under drought stress. **Results:** *B. subtilis* (LDR2) enhanced drought/salt tolerance in wheat crops **Conclusion:** *B. subtilis* confer drought stress tolerance in wheat by enhancing IAA, reducing ACC andABA contents | Barnawal et al. (2014) |
| **Enterobacter ludwigi AffR02 and Bacillus megaterium Mj1212** | *Medicago sativa L.* | **Objective:** To investigate the role of *E. ludwigi* and *B. megaterium* under drought stress conditions. **Results:** The application of *E. ludwigi* and *B. megaterium* significantly recovered the growth attributes (shoot/root length, Fresh/dry weight, shoot diameter and chlorophyll content) in post-drought stressed alfalfa plants. Moreover a significant decrease in electrolyte leakage and ABA content while increase in RWC were observed. Different antioxidants showed an increase in phenolic content, DPPH scavenging activities and total flavonoid content in bacterial inoculated alfalfa plants. An increase in K, P, Ca and Mg content were observed in post-drought stressed *E. ludwigi* and *B. megaterium* inoculated plants. **Conclusion:** *E. ludwigi* and *B. megaterium* have capability to mitigate drought stress while further studies are needed in the field conditions. | Kang et al. (2021) |

(Continued)
Table 2. Continued.

| Microorganism | Plant used | Objectives, Results and Conclusion | Reference |
|---------------|------------|------------------------------------|-----------|
| *Pseudomonas fluorescens* DR7, *P. fluorescens* DR11, *P. migulae* DR35 and *Enterobacter hormaechei* DR16 | *Setaria italica* | **Objective:** To evaluate the role of PGPR under drought stress  
**Results:** Bacterial strain were isolated and four isolates were selected based on their drought stress tolerance, exopolysaccharide and ACC deaminase production. Inoculation of all these strain enhance seedling growth under drought stress via colonize the root adhering soil, increase soil moisture content. | Niu et al. (2018) |
| *Bacillus subtilis* HAS31 | *Solanum tuberosum* | **Objective:** To investigate the role of *Bacillus subtilis* HAS31 under drought stress  
**Results:** Inoculation of isolate *Bacillus subtilis* HAS31 to drought tolerant and drought sensitive potato were applied after 1 days of germination and potato plants were exposed to different soil relative content for 7 days at tuber initiation stage. A significant increase in growth attributes along with tuber weight and yield were observed in HAS31 inoculated potato plants under drought stress. PGPR-HAS31 maintain higher soluble sugar and enzymatic activities such as CAT, POD and SOD under drought stress. | Batool et al. (2020) |
| *Arbuscular mychorrhizal fungi* and PGPR | *Nicotiana tabacum* | **Objective:** To investigate the role of *Arbuscular Mychorrhizal Fungi* and PGPR under drought stress  
**Results:** Glomus versiforme and PGPR Bacillus methylotrophics were inoculated to tobacco plants subjected to drought stress. Results showed drought stress reduce the physiological attributes, while increase in growth, chlorophyll and PSII were observer in co-inoculated AMF+PGPR tobacco plants. Furthermore, reduce in EL and LPO while enhance in phenol and flavonoids content were also observed in inoculated tobacco plants. | Begum et al. (2022) |
| *Mycorrhizal fungi* and *Rhizobium* sp. | *Glycine max* | **Objective:** To investigate the role of *Mycorrhizal fungi* and *Rhizobium* sp. to improve crop productivity.  
**Results:** Co-inoculation of soybean with mycorrhizal consortium have significant impact on soybean biomass, leaf RWC, EL under drought stress by increasing soybean pod number, seed fresh weight, no of seed per pods. | Igiehon and Babalola (2021) |
| *Glomus mosseae* and *Azobacter*+ *Azospirillum* | *Juglans regia* | **Objective:** To investigate the role of AMF and PGPR under drought stress  
**Results:** Application of consortium (AMF+PGPB) alleviate the negative effects of drought stress and significantly increase total phenolic content, total sugar content as well as antioxidant activities in walnut plant under drought stress. | Behrooz et al. (2019) |
| *Waterlogging stress* | *Pseudomonas veronii* KJ | *Sesamum indicum* L. | **Objective:** To evaluate the role of ACC deaminase producing *Pseudomonas veronii* under waterlogging stress  
**Results:** Isolate KJ was used as bio-inoculant and monitored different plant growth and developmental characteristic of sesame plants including fresh/dry biomass, root/shoot length and chlorophyll content under water logging stress.  
**Conclusion:** Waterlogging condition adversely affects different physiological aspects of Sesame plants, however, plants inoculated with ACC deaminase producing *P. veronii* alleviate the stressful condition and contribute to plant growth and development. | Ali et al. (2018b) |
| *Rhodobacter sphaeroides* KE149 | *Vigna angularis* | **Objective:** To evaluate the role of *R. sphaeroides* under waterlogging stress.  
**Results:** Application of isolate *R. sphaeroides* significantly improve plant morphological attributes by decreasing endogenous ABA, JA content while increase SA under water stress. Proline, methionine, Ca, Mg and K content were significantly increased whereas Na content were reduced in treated adzuki bean plants under waterlogging stress.  
**Conclusion:** *R. sphaeroides* regulate phytohormones, amino acid and nutrient uptake system in adzuki bean under waterlogging stress, therefore phytohormones producing bacteria for developing biofertilizer to mitigate waterlogging stress. | Kang et al. (2020b) |
| Microorganism | Plant used | Objectives, Results and Conclusion | Reference |
|--------------|------------|-----------------------------------|-----------|
| Trichoderma asperellum MAP1 | Triticum aestivum | **Objective:** To evaluate the role of endophytic Trichoderma asperellum MAP1 in waterlogging stress. | Rauf et al., 2021 |
| **Heavy metal stress** |  |
| Enterobacter ludwigii SAK5 and Exiguobacterium indicum SA22 | Oryza sativa | **Objective:** To evaluate the role of Enterobacter ludwigii SAK5 and Exiguobacterium indicum SA22 in heavy metal stress. | Jan et al. (2019) |
| Pseudomonas psychrotolerans CS51 | Cucumis sativus | **Objective:** To elucidate the role of P. psychrotolerans under heavy metals stress. | Kang et al. (2020a) |
| Enterobacter ludwigii GAK2 | Oryza sativa | **Objective:** To investigate the role of E. ludwigii GAK2 under heavy metal. | Adhikari et al. (2020) |
| Bacillus cereus ALT1 | Glycine max | **Objective:** To investigate the role of B. cereus ALT1 in the mitigation of heavy metal stress. | Sahile et al. (2021) |
| Bacillus gibsonii and B. xiamenensis | Sesbania sesban L. | **Objective:** To evaluate the role of Bacillus gibsonii and B. xiamenensis role in heavy metal stress. | Zainab et al. (2021) |
| Glomerella truncate, Phomopsis fujushii | Solanum nigrum | **Objective:** To investigate the role of Cd tolerant endophytic fungi under Cd stress. | Khan et al. (2017) |

(Continued)
### Table 2. Continued.

| Microorganism                      | Plant used          | Objectives, Results and Conclusion                                                                                                                                                                                                 | Reference               |
|-----------------------------------|---------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------|
| Gliocladium cibotti               | Glycine max         | **Objective:** To evaluate the role of G. cibotti on crop plants under heat stress                                                                                                                                                   | Ismail et al. (2020)     |
|                                   |                     | **Results:** Association of G. cibotti with soybean and sunflower enhance chlorophyll, total biomass and plant height under heat stress. Furthermore, stress hormone ABA were inhibited while increase in ROS scavenging antioxidants CAT, SOD, POD and GR were increased under heat stress in G. cibotti inoculated sunflower and soybean plants. |                          |
|                                   |                     | **Conclusion:** G. cibotti can be used to mitigate the adverse effects of heat stress on crops                                                                                                                                         |                          |
| Thermomyces lanuginosus           | Cullen plicata      | **Objective:** To evaluate the role of endophytic T. lanuginosus in plant growth promotion under heat stress                                                                                                                                                     | Ali et al. (2019)        |
|                                   |                     | **Results:** The fungus had an effective growth promoting activity on its host plant and increase plant resistance to heat stress via change in different antioxidants (CAT, POD, SOD).                                                                                       |                          |
|                                   |                     | **Conclusion:** Thermophilic T. lanuginosus enhance heat stress tolerance and support plant growth and development                                                                                                                |                          |
| Thermomyces                       | Cucumis sativus     | **Objective:** To investigate the role of Thermomyces on cucumber under heat stress                                                                                                                                                   | Ali et al. (2018a)       |
|                                   |                     |                                                                                                                                                                                                                                     |                          |
| **Arbuscular mycorrhizal fungi**  | *Helianthus annuus* L. | **Objective:** To investigate the role of fungal endophytes in association of AMF and *Helianthus annuus* L. under heat stress.                                                                                                               | EF et al. (2015)         |
|                                   |                     | **Results:** AMF mitigated Cd stress in *Helianthus annuus* L.                                                                                                                                                                        |                          |
|                                   |                     | **Conclusion:** AMF mitigated Cd stress in *Helianthus annuus* L.                                                                                                                                                                       |                          |
| **Temperature stress**            | *Helianthus annuus* L. | **Objective:** To investigate the role of Bacillus cereus SA1 and humic acid under heat stress                                                                                                                                       | Khan et al. (2020a)      |
| Bacillus cereus SA1               | *Helianthus annuus* L. | **Results:** The combine application of thermotolerant plant growth promoting SA1 and humic acid significantly improve tomato biomass and chlorophyll content under heat stress. Further increase in SA, different antioxidant (APX, SOD and GSH) and ion uptake (Fe, P and K) were observed in treated plants under heat stress. Moreover heat stress transcription factor SiHsfA1a were upregulated in SA1+HA treated plants. |                          |
|                                   |                     | **Conclusion:** Combine application of B. cereus SA1 and HA showed significant improvement in tomato plants under heat stress.                                                                                                                                 |                          |
| Bacillus tequilensis SSB07        | *Glycine max*       | **Objective:** To evaluate the role of *Bacillus tequilensis* SSB07 in the mitigation of heat stress                                                                                                                                      | Kang et al. (2019)       |
|                                   |                     | **Results:** Bacillus tequilensis SSB07 improve the growth of Chinese cabbage seedlings and produce gibberellins as well as indole-3-acetic acid and abscisic acid. SSB07 increase the shoot length and biomass, leaf development, and photosynthetic pigment, increased the endogenous jasmonic acid and salicylic acid contents and down-regulate ABA level. |                          |
|                                   |                     | **Conclusion:** Bacillus tequilensis SSB07 counter the negative effects of heat stress on crops                                                                                                                                               |                          |
| Bacillus cereus SA1               | *Glycine max*       | **Objective:** To investigate the role of thermotolerant plant growth-promoting microbes under heat stress                                                                                                                                           | Khan et al. (2020b)      |
|                                   |                     | **Results:** Different microbes were screen for PGP traits and thermotolerance and select isolate SA1. Isolate SA1 produce IAA, GA, organic acid and upon inoculation to soybean plants under heat stress increase the growth and chlorophyll content by decreasing stress hormone ABA and increase SA along with different antioxidant (POD, SOD, CAT) and different amino acid contents. Furthermore increase in expression of heat shock protein (GmHSP) and stress responsive genes GmLAX3 and GmAKT2 were observed in SA1 inoculated soybean plants. |                          |
|                                   |                     | **Conclusion:** Bacillus cereus SA1 mitigate the adverse effects of heat stress                                                                                                                                                        |                          |
wheat seedlings. As part of an integrated crop management (ICM) system, MPBs are a key tool for modern agriculture, improving the sustainability and resilience of agriculture. Hamid et al. (2021) reported that MPBs promote plant growth through a variety of direct and indirect mechanisms. Nutrient acquisition, siderophores, organic acids, growth regulators, and stress-responsive phytohormones have been well reported. These factors alleviate abiotic stresses through various modes of action and induce plant defenses.

Role of MPBs in heavy metals stress tolerance

The accumulation of different heavy metals in the soil adversely affects its texture and pH. The change in soil pH and texture consequently reduces crop growth by exerting negative effects on several plant biological processes. Recent reports have revealed that heavy metal stress affects cytoplasmic enzyme inhibition, causes cell structural damage, inhibits antioxidant enzymes, and induces reactive oxygen species (ROS) scavenging enzymes. Several MPBs have been reported to mitigate the deleterious effects of heavy metals and to enhance crop growth and productivity. MPBs inhibit the movement and saturation of heavy metals in various parts of crops. They alter metabolism via adsorption, chelation, and precipitation. MPBs release EPS substances that possess a considerable number of anion-binding sites that help remove heavy metals from the rhizosphere of plants via biosorption (Ahmad Wani et al. 2008, Ahmad et al. 2014, Ain et al. 2016, Latef et al. 2020).

MPB technologies could be viable alternatives to traditional methods for the removal of different heavy metals from agricultural soils. Desoky et al. (2020) studied heavy metal-resistant bacteria isolated from industrial effluents and their potential as heavy metal-stressed spinach plant bioremediators. Three isolates were selected because of their strong resistance to heavy metals. The isolates were identified as Bacillus subtilis subsp. spizizenii DSM, Paenibacillus jamilae DSM, and Pseudomonas aeruginosa DSM. The application of heavy metal-resistant bacteria improved the tolerance of spinach plant to stressful conditions by increasing the growth and development of the crop plants.

Role of MPBs in waterlogging stress tolerance

Plants under waterlogging stress (hypoxia or anoxia) switch from aerobic respiration to anaerobic fermentation. These oxygen-deficient conditions lead to metabolic disturbances as well as physiological and morphological changes. According to available literature, most genes expressed during waterlogging stress are likely involved in the production of enzymes known to play a role in the formation of fermentative pathways. This metabolic shift occurs in plants and provides a constant supply of adenosine triphosphate (ATP). Plants respond to waterlogging stress in a variety of ways, such as by reducing stomatal conductance and the net carbon dioxide assimilation rate. Furthermore, plants growing under stressful conditions frequently suffer from oxidative damage caused by ROS. Similar to other abiotic stressors, ROS degrade membrane integrity and photosystem II efficiency, resulting in a significant decrease in net photosynthetic rates (Ashraf 2012, Kang et al. 2020).

Various strategies have been employed to mitigate unwanted effects of waterlogged conditions on different crops. However, recent studies have revealed that the
application of MPBs is more productive than other approaches. Ethylene is produced in response to waterlogging stress, indicating that plants also produce more ACC synthase, resulting in a considerably higher level of ACC exudation into the rhizosphere (Glick 2014). Most MPBs produce ACC deaminase and IAA, which promote root exudation and enhance plant growth and development (Figure 1). MPBs that use exuded ACC have a competitive advantage over other microorganisms. Khan, et al. (2018) applied *Pseudomonas veronii* as an MPB under waterlogged conditions and recorded sesame plant growth and development, including leaf chlorophyll, fluorescence signals, chlorophyll concentration, root and shoot length, and fresh and dry biomass in stressed versus unstressed plants. Waterlogging stress-related damage was significantly reduced in plants treated with *P. veronii*. Owing to its potential to minimize waterlogging stress-related damage in sesame plants, the rhizobacterium *Pseudomonas veronii* may be considered as a valuable addition to the consortium of MPBs. Similarly, a recent study reported the application of endophytic *Trichoderma asperellum* (strain MAP1) on wheat growth under waterlogging stress and concluded that *T. asperellum* contributes to the alleviation of waterlogging stress damage in wheat plants by producing phytohormones and secondary metabolites, supporting the plant’s antioxidant system, influencing the physiology by polyamine production, and modulating gene expression (Rauf et al. 2021). Plant endophytism and crop biostimulation are interconnected. White et al. (2021) reported a variety of MPBs that are widely used in agriculture and demonstrated their action under endophytic associations or by stimulating soil microbe absorption. They also support the role of bacterial endophytes as MPBs in sustainable agricultural practices.

### Synergistic effect of fungi and bacteria as plant biostimulants

The application of microbial consortia is an emerging frontier in the field of crop biology that enables plant microbiome engineering, where microbial consortia are rationally designed combinations of microbes that are capable of producing desired effects on the growth and development of plants (Kong et al. 2018). Ruzzi and Aroca (2015b) showed that plant growth-promoting bacteria and fungi can be inoculated for their desired effects and are considered the most promising MPBs. In natural environments, plants are associated with different fungal and bacterial species, and various endophytic, epiphytic, and rhizospheric microorganisms are involved in their response to stress conditions. Thus, this concept has been exploited to develop microbial consortia for the growth and development of crop plants under adverse environmental conditions. Microbial consortia are composed of compatible beneficial microbial strains with different modes of action to provide broad-spectrum usage for crop improvement. Prior to application, a genetically diverse group of strains capable of acclimatizing under varied environmental conditions is selected (Bradačová et al. 2019). Kong et al. (2018) reported basic insights into the structure, dynamics, and ecology of interacting microbial species by characterizing the role of synthetic microbial consortia and their applications.

According to CMC-7, plant MPBs may be a single microbe or consist of a consortium of microbes that includes different genera, such as *Rhizobium* spp., *Azotobacter* spp., *Azospirillum* spp., and mycorrhizal fungi. Thus, the synergistic effects of fungal and bacterial biostimulants are important for the normal growth and development of plants, even under abiotic stress conditions. The term biostimulant is broader than biofertilizers as MPBs induce most of the natural processes, such as augmenting nutrient uptake, reducing water use efficiency, tolerating environmental stresses, and promoting plant growth, and can be formulated with a single strain of bacteria or fungi or in a combination of bacteria or fungi. Similarly, the efficacy of MPBs depends on several factors, including the crop, soil, product used, and mode of application. Additionally, some recent reports revealed the potential of MPB consortia as an agricultural probiotic that are involved in various mechanisms such as carbon exchange, enhancing the capacity of plants to absorb more nutrients, and counteracting the negative effects of different stressors (Kong et al. 2018, Woo and Pepe 2018).

### Conclusion and future perspective

Abiotic stressors are a major threat to global food security as they negatively impact crop development, physiology, and biochemical functions, affecting crop production and quality. The application of MPBs allows plants to cope with various environmental challenges in an environmentally acceptable manner. MPBs in the root microbiome stimulate plant growth by regulating phytohormone synthesis, osmo-lytes, organic acid production, and nutrient uptake as well as by enhancing the antioxidant system and upregulating stress tolerance genes. However, more research at the molecular level is needed to fully understand the mechanism through which MPBs confer stress tolerance. Consequently, further research into the development of even more stress-tolerant MPBs and their application under field conditions will be critical in addressing global food security issues.

The legislative procedures for MPBs follow diverse legal regulations that must be unified globally. There is a great deal of variation in the risk and efficacy evaluation criteria, and there is a lack of a clear and consistent classification. Thus, the commercial registration process of MPBs requires harmonized international legislation as the regulatory situation of MPBs is complex and a harmonized framework is a prerequisite. The application of a single strain (bacterial/fungal) as an MPB appears to be effective, while a consortia of MPBs exerts synergistic effects. Therefore, it can be considered as a preferable alternative. Tabacciioni et al. (2021) recently reported on beneficial microbial consortia as plant biostimulants for sustainable agriculture. They used compatible multi-strain species with different functions and analyzed the role of bioactive compounds in the efficiency of microbial consortia. They concluded that bioactive compounds enhance the growth and efficiency of microbial consortia, and that microorganisms in the consortia act synergistically. During field trials, a single strain may be ineffective, particularly under stressful conditions. Hence, the use of compatible microbial consortia with multi-plant growth-promoting traits could represent a more pragmatic approach to enhance the efficiency of microbial communities and promote plant growth for sustainable agriculture, even under abiotic stress conditions.

COVID-19 has posed serious challenges worldwide. Researchers are struggling to decrease the adverse impacts of COVID-19 on all sectors, including crop productivity, as
the global food supply is under the threat from food insecurity (Mthembu et al. 2022). The global biostimulant market was valued at $2638 million in 2020 and is projected to reach $5040 million by 2026, registering a compound annual growth rate of 11.71% during 2021–2026. However, the COVID-19 pandemic has substantially affected market dynamics. Similarly, the governments of major agricultural countries have taken different measures to protect their agricultural sectors and are trying to alleviate the adverse effects of environmental stressors and enhance crop productivity. In this regard, MPBs are critical to the future success of the agricultural industry in terms of encouraging organic farming and environmental protection.

Disclosure statement
No potential conflict of interest was reported by the author(s).

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