

Chapter 9

Current Approaches for Alleviating Abiotic Stress Tolerance in Crops: Role of Beneficial Microorganisms



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Abstract Global climate change is evolving as a potential threat to the sustainable food security. Abiotic stresses are the most important limiting factors to the agricultural crop productivity. Therefore, exploration of efficient and economical technologies for the alleviation of abiotic stresses in plants are necessary to encounter the food security. The rhizosphere and phyllosphere of plants are colonized by various microorganisms, establishing neutral, detrimental or beneficial associations with their respective host plants. The beneficial microorganisms sustain various physiological activities in plants under extreme climatic conditions. They also promote the abiotic stress tolerance of plants, thereby improving plant growth and productivity. Therefore, amelioration of abiotic stresses in crop plants by using the microorganisms is opening a promising avenue in enhancing the agricultural productivity. The chapter summarizes the role of beneficial microorganisms in enhancing the crop plants' productivity through alleviation of abiotic stresses for the agricultural sustainability.

Keywords Abiotic stress · Crop · Microorganism · Heavy metals · Reactive oxygen species · Plant growth-promoting bacteria

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9.1 Introduction

The sessile nature of plants often compels them to confront environmental challenges caused by the universal climate change. Environmental stresses including salinity, drought, extreme temperatures and heavy metal toxicity have devastating impacts on the growth and yield of major crop plants throughout the world. Abiotic stress frequently affects around 90% of the agricultural lands resulting in above 70% loss of global crop productivity (Mantri et al. 2012). Current climate prediction models indicate a gradual increase in the ambient temperature with erratic rainfall to affect various ecosystems posing a considerable threat to the future food security. According to the Food and Agriculture Organization of the United Nations (FAO), the global food production requires to be increased by 70% to meet the food demand for the estimated global population of ~9.7 billion by the year 2050 (F.A.O. (Food and Agriculture Organization of the United Nations) 2017). It is, therefore, a major challenge to take necessary steps to safeguard the abiotic stress-induced loss of agricultural productivity.

Abiotic stresses severely impede the seed germination and fruiting patterns of the agricultural crop plants. Individual or combination of different abiotic stresses induces morphological, physiological, biochemical and molecular alterations in plants that adversely affect the growth, biomass and productivity (Kumar et al. 2009a). Several abiotic stresses also disturb the plant water relations, thereby reducing the water use efficiency. Abiotic stresses increase the overproduction of reactive oxygen species (ROS) including hydrogen peroxide (H_2O_2), hydroxide ions (OH^\cdot), singlet oxygen ($^1\text{O}_2$) and superoxide anion (O_2^-) through enhanced leakage of electrons from the electron transport chain to the molecular oxygen (Basu et al. 2021a). Excessive ROS accumulation in plant cells leads to oxidative damages by oxidizing photosynthetic pigments, membrane lipids, nucleic acids and proteins, thereby inducing the tissue-specific programmed cell death (Nath et al. 2016, 2017; Kapoor et al. 2019; Kundu et al. 2020).

Abiotic stress tolerance in plants is associated with the maintenance of the cellular redox homeostasis mediated by antioxidant defence system-induced ROS scavenging (Dwivedi et al. 2019; Basu and Kumar 2021). The enzymatic antioxidants facilitating the ROS detoxification include superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR) and dehydroascorbate reductase (DHAR) (Basu et al. 2022). The non-enzymatic antioxidants mediating ROS scavenging include ascorbic acid, carotenoids, reduced glutathione (GSH), flavonoids and α -tocopherol. Growth enhancers like proline and soluble sugars also confer abiotic stress tolerance by interfering with the metabolic processes through osmotic adjustment.

9.2 Plant Growth-Promoting Microorganisms

Microbes possess the ability to enhance the plant growth by synthesizing various microbial products. Bacteria derived from the plant rhizosphere have been demonstrated to have beneficial effects on the roots of their host plants. The presence of plant growth-promoting rhizobacteria (PGPR) on the plant roots has been found to have positive direct and indirect effects on the plant growth with amelioration of various abiotic stresses (Basu and Kumar 2020a). The beneficial microbes can enhance plant growth through the induction of systemic resistance, antibiosis and competitive omission. These rhizospheric microorganisms, with their unique characteristics, diversity and relationship with plants require to be further exploited to address their potential role in abiotic stress tolerance in plants (Prasad et al. 2015). For instance, *Bacillus* species can form endospores that are extremely resilient to harsh environmental conditions and can also secrete metabolites that stimulate plant growth and health. Some *Bacillus subtilis* strains also emit various types of volatile organic compounds assisting plants to recover from stress. *Bacillus* species also secrete exopolysaccharides and siderophores that inhibit the movement of toxic ions and help in maintaining the ionic equilibrium, consequently facilitating the water uptake by plant roots. Thus, the successful application of beneficial microbes provides a model for enhancing abiotic stress tolerance and adaptation to climate change. There is a potential to improve the beneficial interactions between plants and microbes by further evaluation and identification of new microbial isolates having significant effect in the rhizosphere. Technology could be used to identify PGPR that might have a beneficial impact on abiotic stress tolerance, soil fertility, nutrient acquisition and ultimately crop productivity (Basu et al. 2020b). Further research is needed to screen and identify beneficial microbial isolates that form plant-associated microbial communities and enhance overall plant health and vigour. The use of a multidisciplinary approach that includes physiology, molecular biology and biotechnology could provide new prospects and formulations with massive potential to manage abiotic stress in crop plants (Singh and Jha 2017).

Abiotic stress tolerance in crop plants may be achieved through chemical fertilizer applications, breeding programs, tissue culture methods and genetic engineering, which are expensive and time-consuming and have adverse effects on the environment. The use of plant growth-promoting endophytic bacteria (PGPEB) is an alternative and eco-friendly approach for improving agricultural crop production by ameliorating the negative effect of abiotic stresses on economically important plant species throughout the world (Khan et al. 2020). The agricultural, coastal and geothermal plant endophytes can colonize both eudicot and monocot plants conferring abiotic stress tolerance. Abiotic stress tolerance is often correlated with the increased ROS accumulation. The ability of bacterial and fungal endophytes to confer abiotic stress tolerance in plants may provide a novel strategy for mitigating the impacts of global climate change on agricultural crop plant species (Rodriguez and Redman 2008; Godoy et al. 2021) (Fig. 9.1; Table 9.1).

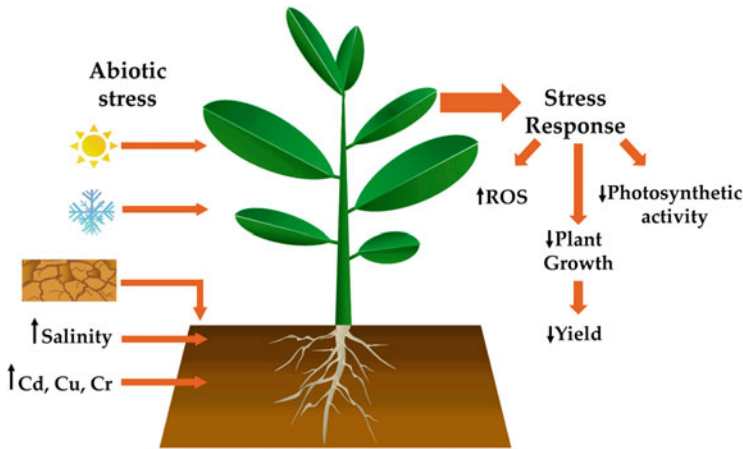


Fig. 9.1 Abiotic stress impact on crop yield (Godoy et al. 2021)

9.2.1 Salinity Stress

Salinity is a major abiotic stress limiting productivity of important agricultural crop species (Basu et al. 2017; Mishra et al. 2021). Salinity-affected area exceeds 20% of the global agricultural land (Fouda et al. 2019). Early exposure to salinity leads to ion toxicity within the plant cells followed by disruption of osmotic balance when the stress persists for longer duration (Kumar et al. 2022a). Combined effect of the ionic and osmotic stresses alters the plant growth and development (Basu et al. 2021b). Salinity also interrupts the ion homeostasis in plant cells and impedes the internal solute balance (Kumar et al. 2009b, 2012). Continuous climate change is rapidly increasing the risk of soil salinization which has been predicted to affect 50% of the arable cropland by the year 2050 (F.A.O. (Food and Agriculture Organization of the United Nations) 2017). It is, therefore, a serious concern to take necessary steps for alleviating the deleterious effect of salinity in crops to encounter the food security.

Plant growth-promoting bacteria (PGPB) play a major role in the alleviation of salinity stress in plants (Basu and Kumar 2020a). The endophytic PGPB induce the growth of the host plants under salinity stress by facilitating the nutrient uptake. They also enhance the antioxidant activities in the host plants under salt stress, thereby maintaining the redox homeostasis. Egamberdieva et al. (2016) have revealed the dual interaction of rhizobia (*Bradyrhizobium japonicum*) and endophytic PGPB (*Stenotrophomonas rhizophila*) to alleviate the salinity stress in soybean (*Glycine max*) plants by inducing their growth and productivity. The PGPB induce salinity tolerance in the host plants by facilitating the nitrogen fixation, phytohormone production, 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, extracellular polymeric substance (EPS) production and biofilm formation (Basu and Kumar 2020b; Kumar et al. 2020a). The siderophore-producing

Table 9.1 Plant growth-promoting microorganism-mediated amelioration of different abiotic stresses

Abiotic stress	Microorganisms	Plants	Reference	
Salinity	<i>Fusarium culmorum</i> (FcRed1)	<i>Oryza sativa</i> , <i>Lycopersicon esculentum</i>	Rodrigue et al. (2008)	
	<i>Pseudomonas putida</i> CW4	<i>L. esculentum</i>	Yan et al. (2014)	
Drought	<i>Curvularia protuberata</i> (Cp4666D) <i>Fusarium culmorum</i> (Fc18, FcRed1)	<i>O. sativa</i> , <i>L. esculentum</i> , <i>Triticum aestivum</i> , <i>Citrullus lanatus</i>	Rodrigue et al. (2008)	
	<i>Colletotrichum magna</i> (path-1)	<i>L. esculentum</i> , <i>Capsicum annuum</i>	Redman (2001)	
	<i>Colletotrichum magna</i> (L2.5)	<i>L. esculentum</i> , <i>Capsicum annuum</i>		
	<i>Colletotrichum musae</i> (927)	<i>L. esculentum</i> , <i>C. annuum</i>		
	<i>Colletotrichum orbiculare</i> (683)	<i>L. esculentum</i>		
	<i>Colletotrichum gloeosporioides</i> (95-41A)	<i>L. esculentum</i>		
Submergence	<i>Pseudomonas putida</i> UW4	<i>Brassica napus</i>	Farwell et al. (2007)	
	<i>Achromobacter xylooxidans</i> <i>Serratia ureilytica</i> <i>Herbaspirillum seropedicae</i> <i>Ochrobactrum rhizosphaerae</i>	<i>Ocimum sanctum</i>	Barnawal et al. (2012)	
Heat	<i>Curvularia protuberata</i> (Cp4666D, CpMH206)	<i>L. esculentum</i>	Rodrigue et al. (2008)	
Chilling	<i>Trichoderma harzianum</i> (OMG16) <i>Bacillus atrophaeus</i> (ABI02)	<i>Zea mays</i> <i>O. sativa</i> <i>T. aestivum</i> <i>Cicer arietinum</i> <i>Solanum melongena</i> <i>C. annuum</i>	Abdel Latef et al. (2020a)	
Heavy metals	As	<i>Micrococcus luteus</i>	<i>Vitis vinifera</i>	Ivan et al. (2017)
	Cu	<i>Bacillus circulans</i> , <i>Paenibacillus polymyxa</i>	<i>Z. mays</i>	Abdel Latef et al. (2020b)
	Cr	<i>Staphylococcus arlettae</i> (MT4)	<i>Helianthus annuus</i>	Qadir et al. (2020)
	Cd	<i>Bacillus siamensis</i>	<i>T. aestivum</i>	Awan et al. (2020)

rhizobacteria have also been reported to ameliorate salinity stress and increasing the iron (Fe) availability in saline soils (Ferreira et al. 2019). Application of plant growth-promoting rhizobacteria (PGPR) has been found to maintain the growth and productivity of French bean (*Phaseolus vulgaris*) (Kumar et al. 2020b). Bokhari et al. (2019) have reported different halophilic phosphate-solubilizing *Bacillus* strains to ameliorate salinity stress in maize (*Zea mays*). The study also determined the involvement of different osmolytes in salinity tolerance of maize plants. Among different *Bacillus* sp. strains, *B. cereus*, *B. subtilis* and *B. circulans* have been found to significantly enhance the growth and fresh weight of the inoculated plants under saline conditions. Two salinity-tolerant strains of *B. circulans* have been found to promote plant growth only in the presence of salt. Co-inoculation of maize plants with *Rhizobium* sp. and *Pseudomonas* sp. has been revealed to show enhanced salinity tolerance with decreased electrolyte leakage and maintenance of leaf water contents (Zelicourta et al. 2013). High abundances of halophilic PGPB *Pseudomonas stutzeri* and *Virgibacillus koreensis* in the rhizosphere of *Calotropis procera* have been shown to induce the plant growth under saline condition (Al-Quwaie 2020). A recent study showed co-inoculation of plant growth-promoting microorganisms *B. cereus*, *B. megaterium*, *Trichoderma longibrachiatum* and *T. simmonsii* to boost simultaneous salinity and drought tolerance in soybean plants by improving seed germination, seedling growth and K⁺ uptake (Bakhshandeh et al. 2020). Another study Abdel Latef et al. (2020a, b) showed inoculation of maize plants with PGPB (*Azospirillum lipoferum* or *Azotobacter chroococcum*) to confer salinity tolerance by reinforcing plant growth and improving physiological activities. Co-inoculation of alfalfa (*Medicago sativa*) plants with salt-tolerant PGPB (*Hartmannibacter diazotrophicus* and *Pseudomonas* sp.) has been shown to enhance salinity tolerance with sustainable plant growth, fresh weight, nodule number, chlorophyll content, relative water content, membrane stability, K⁺/Na⁺ ratio and photosynthetic performances (Ansari et al. 2019). Inoculation of wheat (*Triticum aestivum*) plants with PGPB (*Stenotrophomonas maltophilia*) has shown to ameliorate the salinity stress with increased K⁺ uptake, proline level and antioxidant enzyme activities (Singh and Jha 2017). The PGPB *Burkholderia phytofirmans* has been reported to enhance salinity tolerance in *Arabidopsis thaliana* (Pinedo et al. 2015).

Arbuscular mycorrhizal fungi (AMF) also significantly contribute in the salinity tolerance in plants (Basu and Kumar 2021) (Fig. 9.2). The AMF improve growth, nutrient uptake and productivity of crop plants under salinity stress (Daei et al. 2009). The study showed AMF to enhance the nitrogen and phosphorus uptake in wheat plants under salinity stress. The AMF also increased the gaseous exchange through stomata and improved the respiration and transpiration eventually affecting the water use efficiency of the host plants. The AMF have also been revealed to increase the osmolyte (carbohydrates and electrolytes) concentrations in plant roots to maintain the osmotic equilibrium under salinity stress. The AMF enhance the magnesium (Mg) uptake in host plants, thereby regulating the negative effect of Na on the leaf chlorophyll content (Miransari et al. 2009). Thus, AMF improve the host plants' photosynthetic activities under salinity stress. The AMF also enhance

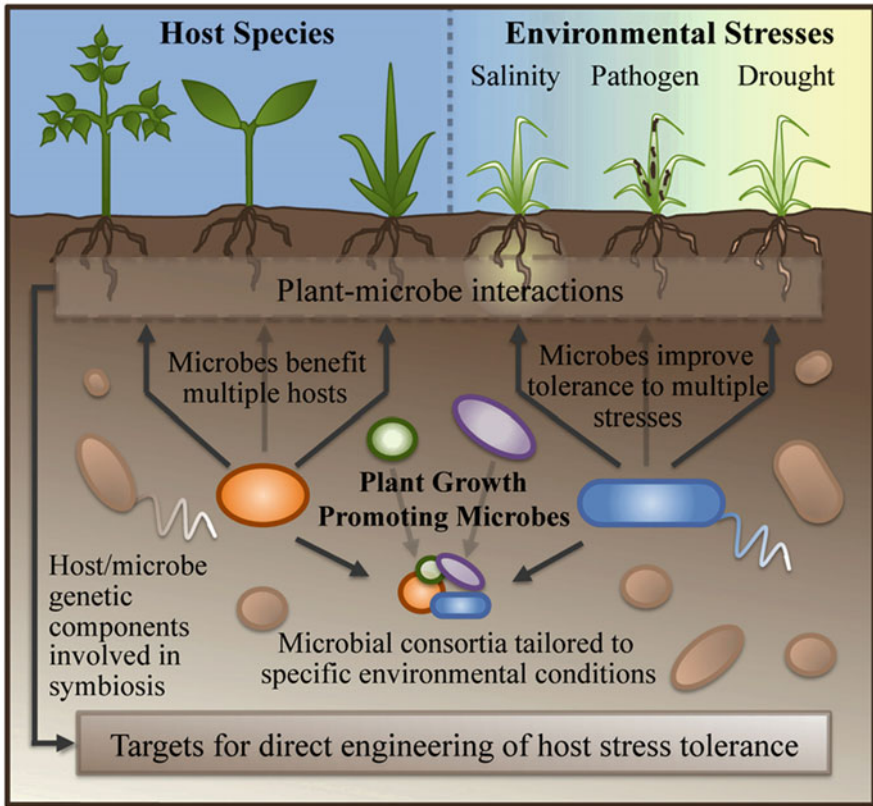


Fig. 9.2 Advantages of plant growth-promoting microbe-mediated approaches to improving stress tolerance in crops (Coleman-Derr and Tringe 2014)

nutrient uptake in roots by increasing the hydraulic conductivity ultimately inducing the root development in host plants (Giri et al. 2003). The AMF enhance the potassium (K) uptake and sustain the K^+/Na^+ ratio leading to improved plant growth under saline conditions. The co-inoculation of PGPR (*Bacillus subtilis*) and AMF (*Claroideoglomus etunicatum*, *Funneliformis mosseae* and *Rhizophagus intraradices*) has been revealed to induce resistance in Talh tree (*Acacia gerrardii*) against the adverse impacts of salinity stress (Hashem et al. 2016). The plants co-inoculated with PGPR and AMF showed increased level of osmoprotectants (proline, phenol and glycine betaine contents) and improved antioxidant enzyme activities with reduced lipid peroxidation.

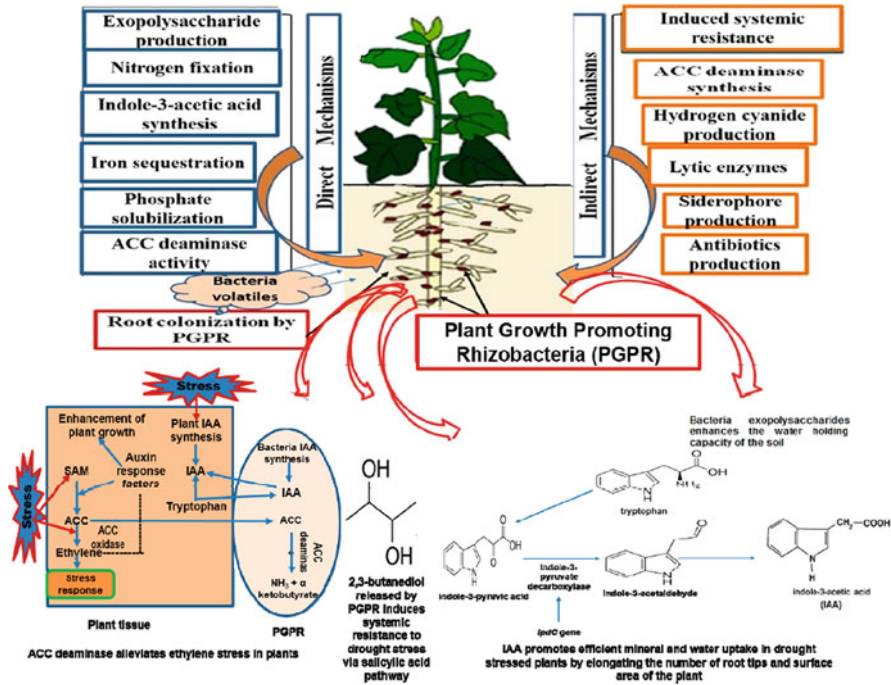


Fig. 9.3 Mechanistic approach-mediated PGPR in alleviating drought stress and plant growth promotion (Ojuederie et al. 2019)

9.2.2 Drought Stress

Drought is also one of the major abiotic stresses limiting the agricultural crop production, thereby causing global food insecurity (Kumar et al. 2020c). Continuous climate change associated with increased air temperature, rainfall anomalies and shifts in the monsoon patterns has been expected to cause frequent drought events throughout the world posing serious threat to the agricultural productivity. Drought stress has been analysed to cause 21, 40 and 50% yield reductions in wheat, maize and rice, respectively (Daryanto et al. 2016). Incidence of drought stress during the pre-anthesis stage shortens the anthesis and the grain filling duration of the cereals, thereby reducing the yield. Drought stress influences the water relations leading to osmotic imbalance in plants (Basu et al. 2021c). It also impedes the plant growth, dry-matter accumulation, canopy temperature, water use efficiency and photosynthetic activities (Basu et al. 2017). Drought also severely impacts the nutrient relations of plants (Garg 2003).

The role of various microorganisms in amelioration of drought stress in plants has been extensively studied (Ojuederie et al. 2019; Fig. 9.3). The PGPR has been shown to enhance the drought stress tolerance in *Acacia abyssinica* (Getahun et al.

2020) and maize (Abdel Latef et al. 2020a, b). Various PGPB strains including *Acinetobacter calcoaceticus*, *Paenibacillus polymyxa*, *Pseudomonas putida* and *P. fluorescens* have been found to enhance drought tolerance in *A. abyssinica*. Drought-tolerant *Rhizobium* sp. has been found to alleviate drought stress in *Sesbania*. Colonization of the roots of wheat plants with *Paenibacillus* sp. and *Bacillus* sp. have been reported to enhance the drought tolerance. The EPS secretion from the microbes provides a suitable environment for chemical reactions, nutrient enrichments and protection against drought by improving the water-holding capacity and fertility of soil through aggregation as observed in *Azospirillum*. Application of *Bacillus subtilis* has been found to be potentially beneficial in enhancing drought tolerance in *Acacia gerrardii* (Hashem et al. 2016). Inoculation of *Sambucus williamsii* with PGPB *Acinetobacter calcoaceticus* has been reported to enhance drought tolerance (Liu et al. 2019). Similarly, another PGPB *Paenibacillus polymyxa* has been found to improve drought tolerance in *Arabidopsis thaliana*. The co-inoculation of two PGPB *Acinetobacter* sp. and *Pseudomonas* sp. has been revealed to enhance drought tolerance in grapevines by maintaining the shoot biomass (Getahun et al. 2020). In pennyroyal plants co-inoculation of *Azotobacter* and *Azospirillum* strains have been reported to impart drought tolerance by increasing the biosynthesis of secondary metabolites. The PGPB *Burkholderia phytofirmans* has been shown to mitigate drought in wheat and maize (Meena et al. 2017). Rhizosphere of cotton (*Gossypium hirsutum*) plants has been reported to predominantly contain *Acidobacteria*, *Actinobacteria*, *Chloroflexi*, *Cyanobacteria*, *Gemmatimonadetes* and *Proteobacteria* under non-stressed conditions (Ullah et al. 2019). However, *Chloroflexi* and *Gemmatimonadetes* have been mostly found in the drought-stressed rhizosphere, which could play an important role to improve drought tolerance in plants. These two phyla have been found to help cotton plants in sustaining various physiological functions under drought stress, thereby conferring drought tolerance. The cluster analyses showed *Acidotherrmus*, *Gemmatimonas*, *Jatrophihabitans*, *Sphingomonas*, *Sphingopyxis* and *Streptomyces* to be relatively abundant in the cotton rhizosphere under normal and drought conditions as compared to the control bulk soil. In addition to the antibiotic and antifungal role of *Streptomyces*, their roles in plant growth promotion under drought stress have also been well documented. Therefore, these bacteria may enhance growth of cotton plants under drought stress. Plant roots change the physical and chemical properties of the soil, and the secretion of root substances modulates microorganisms in the rhizosphere. On the other hand, some microorganisms failed to grow in drought-stressed soils. Some microorganisms adhere to the roots and may subsequently enhance growth and drought tolerance. The soil bacterial community might be important to plants in maintaining essential functions. The PGPB *Pseudomonas fluorescens* and *P. putida* have also been revealed to be exceptional in enhancing drought tolerance in black henbane (*Hyoscyamus niger*) plants through sustainable plant growth, chlorophyll, proline, leaf relative water content and enhanced antioxidant enzyme activities (Ghorbanpour et al. 2013). Higher membrane transport in PGPB has been predicted to enhance salinity and drought tolerance by regulating Na^+/K^+ ratio and H^+ -ATPase of the plasma membrane. Higher

metabolic pathways have also been found to contribute in improved drought tolerance in plants (Ullah et al. 2019).

The AMF symbioses also play an important role in enhancing drought tolerance in plants (Basu and Kumar 2020c). They bind to the soil particles with glomalin and alter the moisture retention capability of soil, thereby inducing the host plants' growth under drought (Auge 2001). Additionally, higher nutrient uptake by the AMF enhances the surface area and density of host plant roots consequently improving their drought tolerance (Subramanian et al. 2006). The AMF facilitates the plant water movement, inducing the hydration and physiological activities of the host plants under drought stress (Porcel and Ruiz-Lozano 2004). The mycorrhizal plants are also able to absorb several forms of nitrogen promoting plant growth under drought conditions. The AMF improve the host plants' biomass under drought stress through increased accumulation of organic products such as glycine betaine, proline, carbohydrates (mannitol, sucrose) and inorganic ions (Cl^- , K^+) (Ruiz-Lozano et al. 2006). Furthermore, the AMF alter the physiology and gene expression of the host plants, thereby enhancing drought tolerance. The mycorrhizal plants also exhibit higher antioxidant enzyme activities under drought stress that enhance drought tolerance through enhanced ROS scavenging and sustain plant growth.

9.2.3 Submergence

Submergence is one of the principal abiotic stresses detrimentally affecting the growth and productivity of important crop species. It severely affects about 10% of the total land worldwide. The flood frequency has been predicted to affect about 42% of the global land by the end of the twenty-first century, thereby impeding the food security (IPCC 2014). Submergence has been characterized by low light intensity, impaired gaseous exchange (Basu et al. 2020a). The O_2 diffusion is reduced 10,000 times under submergence than the normal air leading to hypoxic or anoxic conditions that inhibit the aerobic respiration of plants. Submergence severely affects the physiological activities in plants, including chlorophyll content, membrane stability and photosynthetic gaseous exchange (Basu et al. 2021a). Incidence of complete submergence for more than a week during the early vegetative stage significantly reduces the dry-matter production resulting in dramatic yield loss.

Submergence-induced higher ethylene concentration inhibits plant growth and leads to chlorosis or cell death. Bacterial ACC deaminase has been found to play an essential role in reducing the excessive ethylene level by catabolizing its precursor (ACC) into ammonia and α -ketobutyrate, thereby alleviating the negative effects of submergence (Sasidharan et al. 2017). The ACC deaminase has been firstly isolated from the bacterium *Pseudomonas* sp. and yeast *Hansenula saturnus*. This enzyme was also found in *Pseudomonas chlororaphis* and different strains of *Pseudomonas putida*. The ACC deaminase has also been found to be produced by fungi and endophytic bacteria (Sarkar et al. 2017). The bacterium *P. putida* has been reported to produce ACC deaminase ameliorating the submergence and metal stress in

Brassica napus (Farwell et al. 2007). Co-inoculation of different ACC deaminase-producing PGPR strains including *Achromobacter xylosoxidans*, *Ochrobactrum rhizosphaerae*, *Serratia ureilytica* and *Herbaspirillum seropedicae* have been found to confer submergence tolerance in *Ocimum sanctum* (Barnawal et al. 2012).

9.2.4 Heat Stress

Global climatic changes along with constant elevation in atmospheric temperature severely influence plant growth and productivity of major agricultural crops. During 1979 to 2003, the annual mean maximum and minimum atmospheric temperature has been found to increase by 0.35 °C and 1.13 °C, respectively (Peng et al. 2004). Intergovernmental Panel on Climate Change (IPCC) has predicted the constant weather change to increase the average universal temperature with a frequency of 0.18 °C every decade (IPCC 2014). Short episodes of heat stress coinciding with sensitive developmental stages have been reported to cause a significant reduction in grain yield. Increase in the temperature from 3 to 4 °C can cause a decrease in agricultural crop productivity by approximately 15–35% in Asia and Africa and 25–35% in the Middle East. Heat stress reduces the life cycle of plants through premature ripening which causes declined crop biomass due to lesser accumulation of assimilates (Dwivedi et al. 2017). Heat stress also affects the grain filling duration and the grain filling rate of plants ultimately decreasing the grain yield (Dwivedi et al. 2019).

The role of different PGPB in alleviating heat stress has been widely examined in various crop plants. A study reported the strain of PGPB *Pseudomonas* to enhance the high-temperature (47–50 °C) tolerance of sorghum seedlings. Rhizobacterial isolates have also been found to confer high-temperature (45 °C) tolerance in plants (Getahun et al. 2020). Thermotolerant *Bacillus cereus* has been found to produce biologically active metabolites, such as indole-3-acetic acid, gibberellin and organic acids. Inoculation of *B. cereus* has been reported to confer heat stress tolerance in soybean plants with improved plant growth, biomass, chlorophyll content and reduced abscisic acid (ABA) and salicylic acid (SA) content. The inoculated plants have been found to exhibit increased antioxidant enzyme activities (ascorbic acid peroxidase, superoxide dismutase), glutathione and amino acid contents under heat stress. The PGPB inoculation also augmented the heat stress response and increased heat shock protein (GmHSP) expression in plants. Plant growth-promoting endophytic bacteria (PGPEB) have also been reported to enhance heat stress tolerance in chickpea, wheat, tomato and potato. The PGPEB can synthesize phytohormones that help in increasing heat stress tolerance by enhancing biofilm formation, reducing ABA levels and increasing HSP levels (Khan et al. 2020). Another study showed plant growth-promoting thermotolerant *Pseudomonas putida* to enhance heat tolerance in wheat by improving plant growth, dry biomass, tiller, spikelet and grain formation (Ali et al. 2011). Inoculation has also been observed to improve the cellular metabolite (proline, chlorophyll, sugars, starch, amino acids and proteins)

levels, enhance the antioxidant enzyme activities (SOD, APX and CAT) and reduce the membrane injury under heat stress. The PGPB colonization on the plant root surface has been seen to mitigate the negative effects of climate change on plant growth. A recent study showed the PGPB *Bacillus cereus* to mitigate heat stress in tomato (Mukhtar et al. 2020). Bacterial inoculation has been revealed to significantly promote plant growth and biomass under heat stress. The EPS production and ACC-deaminase activity have been observed to be significantly increased in the inoculated plants. The AMF have been found to ameliorate heat stress in thermophilic plants (Bunn et al. 2009). They extend the extra radical hyphae into the soil and increase the host plants' access to water and nutrients, thereby promoting root growth under heat stress.

9.2.5 Low-Temperature Stress

Low-temperature or chilling stress is one of the major abiotic stresses severely affecting plant growth and hindering productivity of important agricultural crop plants (Liu et al. 2018). Most of the tropical and subtropical crop plants, including rice and maize, are extremely sensitive to chilling stress. Seed germination, physiological and biochemical performances are disrupted under low-temperature stress. Therefore, amelioration of chilling stress in crop plants has become a major challenge to encounter the food security. The PGPM play an important role in this background.

Maize seedlings inoculated with PGPR have been shown to confer chilling tolerance (Abdel Latef et al. 2020a, b). Plants under extreme cold conditions survive either through avoiding supercooling of tissue water or through freezing tolerance (Meena et al. 2017). Inoculation of *Trichoderma* or *Bacillus* is a suitable strategy to improve the chilling tolerance in plants. Although co-cultivation of *Trichoderma* and *Bacillus* strains on artificial growth media was frequently characterized by antagonisms in many plant species including *Oryza sativa*, *Triticum aestivum*, *Cicer arietinum*, *Solanum melongena* and *Capsicum annum*, synergistic beneficial effects were reported after co-inoculation. This included stimulation of seed germination and plant growth promotion in cold and wet soils. In a recent study, Moradtalab et al. (2020) conducted a pre-selection trial with a range of fungal and bacterial PGPM strains based on *Penicillium* sp. with cold-protective properties, a cold-tolerant strain of *Bacillus atrophaeus* and a microbial consortium product (MCP), based on a combined formulation of *Trichoderma harzianum* and *Bacillus* spp. with Zn/Mn supplementation. Inoculation with *T. harzianum* has been observed to promote maize root colonization. The inoculated plants showed increased ABA/cytokinin ratio and increased concentrations of jasmonic (JA) and SA with increased enzymatic and non-enzymatic antioxidant-mediated ROS detoxification. Additional supplementation with Zn and Mn further increased plant growth, shoot IAA and total antioxidants leading to decreased oxidative damage in plants under cold stress. Another study revealed the inoculation of cold-tolerant endophytic bacteria

Pseudomonas vancouverensis and *P. frederiksbergensis* to confer low-temperature (10–12 °C) tolerance in tomato plants (Subramanian et al. 2015). The inoculated plants showed induced expressions of CRT repeat binding factors (LeCBF1 and LeCBF3) under chilling stress. Similarly, PGPEB *Burkholderia phytofirmans* has been reported to provide increased chilling tolerance in *Arabidopsis* (Su et al. 2015).

9.2.6 Heavy Metal Toxicity

Heavy metals (HMs) are the food chain contaminants affecting the growth and productivity of crop plants (Kamal et al. 2010; Thakare et al. 2021; Sonowal et al. 2022). Continuous climate change has been predicted to exaggerate the HMs (arsenic, cadmium, lead, chromium, mercury) contamination in the soil causing substantial yield loss of major crop plants (Kumar et al. 2022b). The excessive intake of HMs by the crop plants also impairs the growth, photosynthetic activities, mineral nutrition and metabolic reactions in plants (Kumar et al. 2021). It is, therefore, a serious worldwide concern to take necessary steps to counteract the problem of HMs toxicity in crop plants (Sarkar et al. 2022).

Numerous studies have shown the PGPR to confer HM tolerance in different crop species. A recent study showed Cd toxicity to decrease the abundance of *Actinobacteria* in the rhizosphere of *Brassica napus*, whereas increased in the rhizosphere of *B. juncea*. In the phyllosphere of *B. napus*, abundance of *Rhodanobacter* sp., *Rickettsia* sp. and *Massilia* sp. has been found to be increased, whereas *Acinetobacter* sp., *Achromobacter* sp. and *Buchera* sp. have been found to decrease under Cd toxicity. The *B. juncea* phyllosphere showed increase in *Gibbsiella* sp., *Lysobacter* sp. and *Stenotrophomonas* sp., while *Gaiell* sp., *Herbaspirillum* sp. and *Telluria* sp. were found to decrease under Cd toxicity (Du et al. 2021). The PGPR has shown *Bacillus anthracis* to confer Cd tolerance in *Sesbania sesban* through higher seed germination (Ali et al. 2021). Another study showed the PGPR strains *Bacillus circulans* and *Paenibacillus polymyxa* to enhance copper tolerance in maize plants (Abdel Latef et al. 2020b). The PGPR strain *Staphylococcus arlettae* has been shown to alleviate chromium toxicity in sunflower plants by restricting its uptake and strengthening the plant antioxidant defence system (Qadir et al. 2020). *Bacillus siamensis* has been shown to improve Cd tolerance in wheat plants by restricting the Cd accumulation and enhancing the antioxidant defence system (Awan et al. 2020). Inoculation of PGPR *Micrococcus luteus* has been shown to impart arsenic (arsenite) tolerance in grapevine with increased biomass and antioxidant potential (Ivan et al. 2017).

9.3 Conclusion

Soil microorganisms are directly and indirectly beneficiary for the agricultural crop plants. Application of the PGPM is widely studied in amelioration of various abiotic stresses like salinity, drought, heat, cold and heavy metals, which severely affect plant growth, physiological activities and agricultural productivity. However, most of the studies are restricted to the laboratory conditions. Therefore, the studies should be executed under the field conditions for sustainable agricultural productivity to keep pace with both the increasing population and continuously changing climate.

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