Rhizospheric Interactions for Abiotic Stress Mitigation

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Edited by

Arvind Kumar Rai, Priyanka Chandra,
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TABLE OF CONTENTS

CHAPTER ONE

SIGNIFICANCE OF PLANT GROWTH PROMOTING RHIZOBACTERIA IN SUSTAINABLE AGRICULTURE UNDER EXTREME ENVIRONMENT

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Abstract

The intricate relationship between microbes, plants and soil forms the foundation of sustainable agriculture, especially in extreme environments where conventional farming practices face significant challenges. In extreme environments, characterized by factors such as drought, nutrient deficiency and salinity the interplay between plants and specialized microbial communities becomes crucial. Beneficial microbes, including plant growth-promoting rhizobacteria (PGPR), mycorrhizal fungi and nitrogen-fixing bacteria, actively participate in nutrient cycling, facilitate stress tolerance, and contribute to soil fertility. Different stress conditions have a wide range of effects on plant morphology, biochemistry, physiology and gene regulation. The key impact of these stresses comprises the loss of soil microbial diversity, loss of soil fertility and competition for nutrients. Intensive application of agro-chemicals has ruined soil fertility, caused environmental pollution and reduced crop productivity. Therefore, to ensure sustainable agricultural production, alternative eco-friendly measures such as the requisition of PGPR, organic inputs *etc*., need to be adopted. This chapter highlights the significance of harnessing soil-plant-microbe interactions as a strategic approach to alleviate the adverse effects of extreme environmental conditions on crop production. By deciphering the intricate signalling pathways, biochemical processes, and genetic adaptations involved in these interactions, innovative agricultural practices can be developed.

Keywords: Abiotic stress, Biotic stress, Mycorrhiza, Sustainability, PGPR.

Introduction

The global population is rapidly increasing and is projected to reach 8.9 billion by 2050 (Singh et al 2011). To gratify the demand of food for such a huge population is a major task at present. The escalating threat of climate change continues unabated and use of agro-chemicals (declined soil health) have made it more challenging. The acceleration of global climate change is a result of an increased occurrence of multiple abiotic stresses, including desertification, salinity, drought, shortage of fresh water sources, flooding, high and low temperatures. Additionally, biotic stresses such as phyto-pathogens are also becoming more prevalent, further degrading agricultural productivity to an irreversible level (Mumtez et al 2022; Cao et al 2023). Various biotic and abiotic stresses perpetually impact the soil ecosystem which directly alters soil fertility, health and ultimately crop productivity. Drought, salinity, temperature and heavy metals are foremost stress factors related to climate change. The abiotic and biotic stresses cause 30 to 50% of losses to agriculture productivity respectively (Kumar and Verma 2018).

Different stress conditions have a wide range of effects on plant morphology, physiology, biochemistry and gene regulation. The major impact of these stresses is the loss of soil microbial diversity, loss of soil fertility and competition for nutrients. The extensive use of agrochemicals has led to the deterioration of soil fertility, environmental pollution and reduced crop productivity. Therefore, to ensure sustainable agricultural production, alternative eco-friendly measures such as application of PGPR, organic inputs *etc*. need to be adopted. PGPR are rhizobacteria inhabiting plant rhizosphere and benefiting the growth and development of plants either through direct mechanisms such as phyto-hormone production, increased nutrient availability or by indirect ways, such as disease suppression by antibiosis, lytic enzymes production and induced systemic resistance (ISR) (Glick 2014; Prasad et al 2021; Choudhary et al 2019). Various genera of *Bacillus*, *Pseudomonas*, *Burkholderia*, *Variovorax*, *Klebsiella*, *Azospirrilum*, *Azotobacter* and *Serratia* are termed as PGPR which promotes the plant growth and development under stress or normal conditions (Kumar and Verma 2018). PGPR have been used globally for several years as biofertilizers owing to their significant positive effects on crop productivity and a span of biotic and abiotic stress tolerance (Upadhyay et al 2012). Several researchers have reported the plant growth-promoting activities of rhizobacteria under drought and salinity stress conditions in different crops (Timmusk et al 2014; Cohen et al 2015; Sarma and Saikia 2014; Singh et al 2017; Vaishnav et al 2015; Narwal et al 2018, Renjit et al 2020).

Plants confront a multitude of challenges, biotic and abiotic, stemming from inherent soil-related factors and human-induced activities. Crop production settings, influenced by a range of factors, frequently subject crops to diverse abiotic stresses. As a consequence, the plants' genetic potential in terms of yield and quality is often hindered (Selvakumar et al 2012). Enhancing stress tolerance in plants, vital for their growth and survival, can be achieved by involving stress-tolerant microorganisms, especially PGPR and Arbuscular Mycorrhizal Fungi (AMF) (Nadeem et al 2014; Narwal et al 2021). Under challenging circumstances, microorganisms employ various direct and indirect mechanisms to stimulate plant growth. These mechanisms encompass a range of biochemical and molecular adjustments that prove advantageous for plant growth and development amidst stress. Notably, PGPR assumes a vital role in multiple processes for example nitrogen fixation, nutrient solubilization (phosphate, potash, zinc, iron, *etc*.), nutrient and water uptake, antibiotic production, hydrolytic enzyme production, and the synthesis of growth factors. Additionally, PGPR aids in the decomposition of decomposed material, providing direct or indirect benefits to enhance plant growth and development. Numerous additional mechanisms, including nutrient mobilization, exo-polysaccharide (EPS) production, rhizobitoxin production, and heavy metal detoxification, contribute to the plant's ability to withstand adverse climatic conditions.

Rhizobitoxin, by inhibiting ethylene production, fosters plant growth and development even in unfavourable circumstances. Furthermore, PGPR exhibits the potential to support plant growth and development during challenging conditions through the action of key enzymes like chitinase, glucanase, and ACC-deaminase (Kumar et al 2009). Furthermore, certain bacteria possess sigma factors that play a crucial role in modifying gene expression under stress, enabling them to counteract harmful effects effectively (Gupta et al 2013). *Bacillus* and *Paenibacillus*, two types of plant growth-promoting bacteria, contribute to plant growth and health through three distinct pathways. Firstly, they enhance host plant nutrition and growth. Secondly, they exhibit antagonistic properties against pathogens while stimulating the plant's defence mechanisms. Lastly, these beneficial bacteria play a significant role in promoting sustainable agriculture practices (Govindasamy et al 2010). Implementing sustainable agricultural practices, coupled with the application of stress-tolerant PGPR, can significantly enhance food grain yields and improve their nutritional quality, even amidst a changing climate. Moreover, this approach has the supplementary benefit of reducing the cost of chemical fertilizers and pesticides by approximately 20-25%. By adopting such practices, farmers can not only boost their financial income but also contribute to the production of organic foods and vegetables.

Mycorrhiza, a symbiotic interaction between fungi and the roots of higher plants, represents a crucial aspect that plays a momentous role in supporting the growth and development of plants, particularly under adverse conditions (Narwal et al 2022; Narwal et al 2023). Among mycorrhizal associations in agricultural fields, AMF stands out as the most common type found. Within this symbiotic relationship, the fungal partner plays a crucial role in efficiently cycling, absorbing, and translocating various nutrients for the benefit of the plant. During drought conditions, AMF plays a pivotal role in enhancing water uptake, thereby preventing the desiccation of plant roots. This assistance proves invaluable in helping the plant withstand and sustain itself under water scarcity conditions (Nadeem et al 2014). This chapter focuses on the mechanisms undertaken by various PGPR under biotic and abiotic stress and also covers the role of AMF in stress conditions.

Protection Mechanisms by PGPR under different kinds of Stresses

Abiotic Stress

Different cultivation practices depending on different agro-ecological patterns suffer from a plethora of abiotic stresses. These abiotic stresses can be categorized into two forms depending upon their origin, atmospheric and edaphic. Drought, floods, extremes of temperature, both hot and cold, and intense precipitation are abiotic stresses originating from the atmosphere. Abiotic stresses generated from edaphic factors include chemical and physical aspects of soil. Chemical factors leading to the stress are soil pH, salinity, toxic heavy metals/organic pollutants and poor soil fertility status. Physical factors creating stress conditions are poor soil texture, high compaction, rockiness and slope steepness. In summary, these factors collectively define the water-holding capacity, cation exchange capacity of the soil, and the magnitude of root contact with the soil matrix. As a result, they significantly influence both minor and major features of plant growth and development (Selvakumar et al 2012).

Salinity

Extensive application of synthetic fertilizers and inefficient management of irrigation water has led to increased salinity in the soil. According to FAO (2005), soil salinity is affecting world's agricultural production as it is reducing the irrigated area by 1-2% every year. Soil salinity presents foremost edaphic stress and is severely detrimental to plant growth and development and almost 20% of the world's cultivated area is influenced by soil salinity and is increasing continuously as a result of improper agricultural and irrigation practices (Glick 2014). Toxic levels of ions and osmotic stress in saline soils are responsible factor for poor microbial activity which ultimately affects plant growth and development. Salinity lowers the water potential in soil which makes the nutrient and water uptake difficult for plants. The soil salinity is mainly caused by Na^+, Ca^{2+}, K^+, Cl^- and NO_3^- ions. Salinity negatively affects seed germination, nutrient and water uptake and plant productivity. It also disturbs the physico-chemical and ecological balance of plant (Selvakumar et al 2012). Additionally, salinity also affects biological nitrogen fixation (nodulation process and nitrogenase activity) adversely which has a direct negative impact on crop yield. Soil salinity affects the microorganism functioning and plant growth mainly through ion toxicity and osmotic effects.

Soil salinity poses different deleterious effects on plants *e.g.* due to higher salt concentration, plants' roots cannot uptake the water from soil. Consequently, plants experience a form of drought leading to stunted growth and yield reduction (Tester and Davenport 2003). The plant's physiological processes can be disturbed due to salts like Na^+ and Cl^- which move into the plant system through water and causes lesser growth and severe conditions can result in plant death (Tester and Davenport 2003). Many crucial plant nutrients like N, P, K, Mg *etc.* which are very important for the growth and development of plants, become unavailable due to greater concentration of Na^+ and Cl^- ions (Tester and Davenport 2003). Salinity negatively impacts plant growth by reducing germination, plant vigor and ultimately crop yield. Salinity reduces photosynthetic capacity due to stomatal closure and also decreases the rates of protein synthesis and lipid metabolism (Selvakumar et al 2012). Symbiotic nitrogen fixation is significantly reduced under higher salinity resulting in reduced number of nodules, lower nitrogen fixation rates and hence reduced total nitrogen content in leguminous plants (Sinclair et al 2010).

Researchers have extensively documented the advantageous impact of PGPR inoculation in alleviating salinity stress in various plants. PGPR can enhance plant growth under high salinity conditions through various direct and indirect mechanisms. Direct mechanisms involve the production of phytohormones such as auxin, cytokinin, gibberellins, and ethylene, nitrogen fixation, nutrient mobilization, and siderophore production. These mechanisms contribute to increased root length, surface area, and root number, thereby improving nutrient and water uptake (Hayat et al 2010). PGPR can mitigate the detrimental effects of soil salinity by maintaining an optimal ratio of K^+/Na^+ ions necessary for plant growth under high salt levels (Mayak et al 2004), preserving redox potential (Yancey 2005), accumulating and synthesizing compatible solutes or osmolytes, stabilizing membrane lipids (Bano and Fatima 2009), scavenging free radicals, and inducing transcription factors involved in stress responses (Gupta et al 2012).

Root architecture is greatly affected by the accumulation of salts at the root surface, this in turn less availability and poor uptake of nutrients. Because mass flow of nutrients occurs with water, osmotic stress induced by salt accumulation causes a decrease in diffusion (Chavarria and dos Santos 2012). Reduction in plant growth occurs under salinity stress because of very less photosynthetic activity in the aboveground plant parts which leads to the use of stored photo-assimilates (Gomez-Bellot et al 2013). The inoculation of selected bacterial strains to the roots of sensitive plants results in lateral root development resulting in an enhanced root system and hence enhancing water uptake through the expression of aquaporins which determines the hydraulic conductance at the root surface (Moshelion et al 2015; Qin et al 2016). The salt overly sensitive pathway maintains ion homeostasis during salinity stress. It consists of three proteins, SOS1, SOS2 and SOS3. The SOS mutants are extremely sensitive to salt stress. SOS1 is also referred to as Na^+/H^+ antiporter which removes Na^+ in response to increasing Na^+ cytosolic levels. The Na^+ and K^+ balance is maintained by high-affinity K^+ transporter 1 (HKT1) which obtains Na^+ from xylem in the shoots (Ji et al 2013).

Rhizobacteria produce exo-polysaccharides (EPS) which form a capsule-like protective biofilm layer on the cell surface. These are polysaccharides that can be classified as homo-polysaccharides, consisting of repeated units of the same monosaccharide, or hetero-polysaccharides, containing different monosaccharides. Among the abundant monomers in these polysaccharides are glucose, galactose, and mannose. EPS can be used as seed priming agents that improve the germination of seed resulting in better crop growth and finally greater yields under high salinity conditions (Tewari and Arora 2014). Biofilm formation by PGPR has been identified as an effective strategy for mitigating the harmful effects of salinity stress (Kasim et al 2016). Plant growth-promoting microbes possess the capability to alleviate salt stress by potentially accumulating osmolytes within their cytoplasm. These osmolytes act as a counterbalance to osmotic stress, aiding in the preservation of cell turgor and promoting plant growth. Moreover, microbial exo-polysaccharides bind cations, rendering them unavailable to plants and inducing resistance against salt stress conditions (Vardharajula et al 2011). Plant tolerance to salt stress is primarily attributed to the selective uptake of K^+ ions, a decrease in osmotic potential, reduced electrolyte leakage, and enhanced proline production (Bano and Fatima 2009). PGP microbes can modulate the expression of various genes to enhance plant salt tolerance. Nautiyal et al (2013) reported the upregulation and repression of 14 different genes in rice plants inoculated with the salt-tolerant *B. amyloliquefaciens* NBRISN13 (SN13), resulting in increased growth and salt tolerance. Volatile organic compounds (VOCs) produced by rhizobacteria are low molecular weight, lipophilic compounds with high vapor pressures, which play roles in inter-organism communication, cell-to-cell signalling, and plant growth promotion (Kai et al 2009). They function as signals for development and systemic responses within the same or neighbouring plants. Timmusk et al (2014) found that wheat plants inoculated with *B. thuringiensis* AZP2 exhibited an increase in VOC levels, aiding in plant survival under salinity stress by enhancing photosynthesis and resulting in higher plant biomass. Some PGPR possess ACC deaminase activity. The ACC deaminase enzyme catalyses the transformation of ACC (ethylene precursor) to α-ketobutyrate and ammonia, thereby helping plants overcome salt-induced growth inhibition by reducing ethylene levels. Various PGPR involved in combating soil salinity in different crop plants are listed in Table 1.

Drought Stress

Drought is recognized as chief agriculture problem globally, restricting plant growth and productivity. It affects different growth factors and stress-responsive genes under stress condition. Drought promotes leaf senescence which results in reduced crop productivity (Tiwari et al 2016). Under drought conditions, plants undergo several molecular and physiological changes, such as changes in chlorophyll content, increased ethylene production, damaged photosynthesis framework and reduced photosynthesis (Lata and Prasad 2011). As water plays an important role in carrying nutrients to the roots, nutrient diffusion decreases over short distances during soil moisture deficit and over longer distances, the mass flow of nutrients soluble in water for example NO^{3-}, SO_4^{2-}, Ca, Mg, Si etc. is reduced (Barber 1995). Drought stress can result in the formation of reactive oxygen species (ROS) for example hydrogen peroxide, superoxide and hydroxyl radicals due to the low availability of CO_2 for photosynthesis. ROS can cause the degradation of membrane lipids through lipid peroxidation (Sgherri et al 2000). ROS also acts upon unsaturated fatty acids and unties the cytoplasmic membranes, and ultimately distress the DNA. Drought stress can inflict damage on cells, both directly and indirectly, through the generation of ROS like superoxide radicals and H_2O_2 (Tiwari et al 2016). Drought stress induces the disruption of various biochemical activities within plants. One significant impact is the reduction in nitrate reductase activity, which serves as the rate-limiting step in the nitrate assimilation pathway. This decrease in activity occurs primarily due to the impaired uptake of nitrate from the soil by the roots under drought conditions (Caravaca et al 2005). Drought leads to disordering interactions between roots and microorganisms that play an important role in nutrient acquisition for plants. It also leads to the loss of nutrients from the rooting zone through erosion (Lynch and Brown 2001). Drought stress upsets plant hormone balance by declining the endogenous levels of cytokinin and leading to accumulation of abscisic acid (ABA) in the leaves, hence stimulating stomatal closure (Figueiredo et al 2008). Drought induces excess production of ROS, causing altered redox homeostasis of cells. Increased ROS levels result in oxidative stress responsible for cell damage and ultimately, cell death. An increased level of ROS leads to the disturbance of proteins bound to the membrane, a reduction in membrane fluidity, suppression of protein synthesis, DNA damage, and a decline in enzymatic activities. During stressful conditions, lipids become primary targets as ROS specifically targets polyunsaturated fatty acids found in membrane phospholipids, initiating a process known as lipid peroxidation. Consequently, fatty acids undergo degradation, giving rise to a diverse range of products, including aldehydes (Gill and Tuteja 2010).

Microbes tolerant to drought stress have capability to boost the growth and development of plants under water scarcity. The soil microbiome also undergoes shifts in terms of relative abundance and the drought-tolerant microbiome develops. There is an increase in the ratio of Gram-positive (monoderms- Firmicutes and Actinobacteria) to Gram-negative (diderms- Proteobacteria, Verrumicrobia and Bacteroidetes) bacteria under dry conditions (Hartmann et al 2017; Fuchslueger et al 2016; Chodak et al 2015). The different physiological mechanisms that help bacteria to survive under drought conditions include spore formation and thick cell walls which allow bacteria to remain dormant for unsuitable environmental periods (Acosta-Martínez et al 2014). Microorganisms as developed several mechanisms to survive under water scarcity conditions such as osmolytes accumulation (free amino acids, soluble sugars), exo-polysaccharide production *etc*. Microbes accompanying with plants have several mechanisms to alleviate the harmful effects of water stress on plants and soil. They assist in improving water availability and uptake, nutrient availability and make the environment conducive for the continuous growth of plants. The constructive microorganisms present in the rhizosphere, stimulate plant growth and development through numerous direct and indirect mechanisms: EPS produced by microbes conserve moisture and provide protection against desiccation, mycorrhizal associations where fungal hyphae help in reducing evaporation losses by forming a thick mantle surrounding roots and also improving water uptake from deeper horizons thereby improve drought tolerance in certain plants. The EPS form hydrophilic biofilms that can retain 70 times more amount of water than the original weight of polysaccharide imparting protection against desiccation (Rossi et al 2012). EPS production by PGPR in the course of water stress results in increased shoot growth, in development of a profuse root system and total dry biomass in plants. EPS plays a significant role as emulsifier, offering protection to bio-membranes and effectively neutralizing ROS (Dimitrova et al 2013). As a result, they contribute to enhanced plant nutrition and growth. PGPR ameliorates the negative effects of water deficiency in plants *via* induced systemic tolerance (IST) which encompasses production of phyto-hormones, antioxidants (that cause ROS degradation and protect the cell against oxidative damage), volatile organic compounds, exopolysaccharides (improved soil aggregates and structure) and siderophores (Fe chelation and uptake). Indole Acetic Acid production by PGPR under water deficit conditions results in increased root surface area, thus enhancing nutrient and water uptake (Vacheron et al 2013), consequently, increasing root and shoot biomass for better plant growth and survival under drought conditions. During drought conditions, stimulation of endogenous gibberellins is known to enhance the germination process, stem elongation, sex expression, flowering and senescence (Glick 2014). Cytokinin-producing rhizobacteria encourage shoot growth through cell division, cell enlargement, and also cause stomatal opening resulting in higher shoot biomass and lower shoot-to-root ratio (Selvakumar et al 2012) under drying conditions. Endogenous ABA levels are highly increased to minimize the water loss in the form of transpiration by closing stomata in response to poor water availability. This also mediates root branching which promotes water uptake in plants (Tardieu et al 2010). In response to drought stress, root development and plant growth are negatively affected by the increased levels of ethylene. ACC (1-aminocyclopropane-1-carboxylate) serves as the precursor of ethylene, a plant hormone crucial for various physiological processes. Ethylene is synthesized by plant ACC synthase primarily in roots and is subsequently exuded into the rhizosphere. Some rhizobacteria possess the enzyme ACC deaminase, which plays a vital role in ethylene regulation. ACC deaminase catalyses the hydrolysis of ACC into ammonia and α-ketobutyrate, thereby reducing ethylene levels in plants (Glick 2014). During drought stress, plants often experience increased production of ROS, which can be highly detrimental. To counteract the damaging effects of ROS, plants possess an antioxidant defence system comprising both enzymatic and non-enzymatic components. Enzymatic elements of this defence system include catalase, superoxide dismutase, ascorbate peroxidase, and glutathione reductase, while non-enzymatic elements include molecules such as glutathione, cysteine, ascorbate, and tocopherols (Miller et al 2010). Furthermore, plants respond to stress conditions by producing volatile organic compounds (VOCs). These compounds are emitted from leaves, typically in low concentrations. However, under stress, the level of VOCs increases, triggering defense-responsive mechanisms in plants (Opris et al 2013). This response aids in combating stress and enhancing plant resilience to environmental challenges.

Table 1. PGPR used as inoculants in various crops to mitigate different stresses.

Plant	**Stress Type**	**PGPR Inoculated**	**Mechanism of Action**	**Reference**
Wheat (*Triticum aestivum*)	Drought	*Bacillus thuringiensis*	Production of IAA and ACC deaminase, increase in lateral root density and length, alginate production	Timmusk et al 2014
Maize (*Zea mays*)	Drought	*Azospirillum lipoferum*	Production of endogenous gibberellins	
Lettuce (*Lactuca sativa*)	Drought	*Bacillus subtilis*	Production of cytokinins, higher shoot biomass and reduced root to shoot ratio	Arkhipova et al 2007
Arabidopsis (*Arabidopsis thaliana*)	Drought	*Azospirillum brasilense*	Elevated Abscisic acid (ABA) level, decreased stomatal conductance thus, retarded water loss	Cohen et al 2015
Pepper (*Piper nigrum*)	Drought	*Bacillus licheniformis*	ACC deaminase activity thus reducing ethylene levels and expression of drought responsive genes	Lim and Kim 2013
Mung bean (*Vigna mungo*)	Drought	*Pseudomonas sp.*	Accelerated levels of catalase, peroxidase and superoxide dismutase	Sarma and Saikia 2014
Basil (*Ocimum basilicum*)	Drought	*Azospirillum and Pseudomonas*	Biosysnthesis of soluble carbohydrates and proline	Heidari et al 2011
Arabidopsis (*Arabidopsis thaliana*)	Drought	*Pseudomonas chlororaphis*	VOC caused stomatal closure and induced IST	Cho et al 2008
Wheat (*Triticum aestivum*)	Salinity	*Enterobacter cloacae*	Decreased accumulation of Na^+, Increased uptake of K^+ in roots and shoots, improved water use efficiency	Singh et al 2017
Arabidopsis (*Arabidopsis thaliana*)	Salinity	*Bacillus subtilis*	Down regulation of the high-affinity K+ transporter (HKT1) in the roots, hence reducing Na^+ uptake	Zhang et al 2008

Soyabean (*Glycine max*)	Salinity	*Pseudomenas simiae*	Production of VOCs that upregulate vegetative storage proteins and RuBisCo	Vaishnav et al 2015
Wheat (*Triticum aestivum*)	Salinity	*B. amylolequifaciens* *B. insolitus* *Microbacterium sp.* *P. syringae*	Restricted Na^+ flux through EPS production	Ashraf et al 2004
White clover (*Trifolium repens*)	Salinity	*Bacillus subtilis*	Decreased shoot and root Na^+ accumulation, improved K^+/Na^+ ratio, enhanced chlorophyll content, osmotic potential and cell membrane integrity	Han et al 2014
Wheat (*Triticum aestivum*)	Salinity	*Bacillus subtilis* and *Arthrobacter* sp.	Accumulation of sugars and proline, increased plant dry matter	Upadhyay et al 2011
Soybean (*Glycine max*)	Salinity	*Bradyrhizobium diazoefficiens*, *Bacillus velezensis*	Enhanced plant growth due to increased degree of nodulation by producing larger nodules and enhanced N_2-fixing efficiency	Sibponkrung et al 2020
Rice (*Oryza sativa*)	Salinity	*Bacillus amyloliquefaciens*	Enhances plant growth by inducing metabolic and physiological responses *via* induction of different enzymes	Bisht et al 2020
Barley (*Hordeum vulgare*)	Salinity	*Hartmannibacter diazotrophicus*	Growth enhancement due to increased ACC deaminase activity, increased root dry weight and shoot dry weight	Suarez et al 2015
Rice (*Oryza sativa*)	Salinity	*Bacillus oryzicola*	Salt stress tolerance *via* the SOS1-dependent salt signalling pathway, resulting in the normal plant growth	Baek et al 2020

Wheat (*Triticum aestivum*)	Heat stress	*Pseudomonas aeruginosa*	ACC deaminase activity, increased plant root length, height, relative water content, dry matter, leaf area, chlorophyll content and lower injury to cell membrane	Meena et al 2015
Sorghum (*Sorghum bicolor)*	Heat stress	*Pseudomonas sp.*	Induction of heat shock proteins (HSPs) in leaves, reduced membrane injury, increase in proline, glycine betaine and amino acid content	Ali et al 2009
Wheat (*Triticum aestivum*)	Heat stress	*Bacillus safensis* and *Ochrobactrum pseudogrignonense*	Increased activity of antioxidant enzymes (SOD, CAT), reduced membrane injury, and increase in proline, sugar and amino acid content	Sarkar et al 2018
Tomato (*Solanum lycopersicum*)	Heat stress	*Paraburkholderia phytofirmans*	Improved photosynthetic activity, increase in proline, sugar and amino acid content	Issa et al 2018
Cotton (*Gossypium* spp.)	Heat stress	*Brevibacillus brevis*	IAA, biological nitrogen fixation, ammonia production and antifungal activity at high temperature	Nehra et al 2016
Grapevine (*Vitis vinifera*)	Cold stress	*Burkholderia phytofirmans*	Lowered rate of biomass reduction and electrolyte leakage, enhanced rates of photosynthesis and starch deposition	Fernandez et al 2012
Wheat (*Triticum aestivum*)	Cold stress	*Pantoea dispersa, Serratia marcescens*	P-solubilization, production of IAA, HCN, and siderophore	Selvakumar et al 2007
Wheat (*Triticum aestivum*)	Cold stress	*Pseudomonas lurida*	P-solubilization, production of IAA, HCN, and siderophore	Selvakumar et al 2011
Lentil (*Lens culinaris*)	Cold stress	*Pseudomonas sp. and Rhizobium leguminosarum*	Improved iron, nutrient uptake and growth	Mishra et al 2011

Pepper (*Piper nigrum*)	Cold stress	*Serratia nematidiphilo*	Higher endogenous GA contents, up-regulation of the endogenous ABA levels, reduced the endogenous jasmonic acid and salicylic acid contents	Kang et al 2015
Tomato (*Solanum lycopersicum*)	Cd toxicity	*Pseudomonas aeruginosa* and *Burkholderia gladioli*	Enhanced production of phenolic compounds, osmo-protectants and organic acids	Khanna et al 2019
Wheat (*Triticum aestivum*)	Cd toxicity	*Pseudomonas sp.*	Enhanced growth of wheat due to IAA and ammonia production, P solubilization	Verma et al 2015
Spinach (*Spinacia oleracea*)	Cd, Pb and Zn toxicity	*Pseudomonas sp.* and *Bacillus sp.*	Production of ACC deaminase, siderophores, IAA and P solubilization	Shilev et al 2019
Brassica oxyrrhina	Cu and Zn toxicity	*Pseudomonas libanensis and Pseudomonas reactans*	Production of ACC deaminase, siderophores, IAA and P solubilization	Ma et al 2016
Rice (*Oryza sativa*)	Cd toxicity	*Enterobacter aerogenes*	Nitrogen fixation, P solubilization, IAA production, ACC deaminase activity	Pramanik et al 2018
Alfalfa *(Medicago sativa)*	Cd, Pb and Zn toxicity	*Proteus sp., Pseudomonas sp.* and *Ensifer meliloti*	Biofilm formation, enhanced activity of antioxidative enzymes	Raklami et al 2019

Temperature Stress

The escalation of global warming has amplified the intensity and frequency of temperature stress on plants. Heat stress is characterized by a temperature rise of 10–15 °C above the optimal range, severely impacting plant growth and development from germination to harvest (Ali et al 2022; Ejaz et al 2022; Ding et al 2021). Both high and low temperatures represent significant abiotic stress conditions that profoundly affect plant physiology. Temperature stress induces alterations in various aspects of plant biology, including changes in plasma membrane composition, alterations in water content, disruption of enzyme activity, destabilization of proteins, impaired photosynthesis, compromised cell division, and inhibited plant growth (Shaffique et al 2022; Issa et al 2018; Nehra et al 2016; Sarkar et al 2018). These effects manifest across different stages of plant growth and development, impacting overall productivity and yield. Consequently, understanding and mitigating the detrimental effects of temperature stress are essential for sustaining agricultural productivity in the face of climate change.

High-Temperature Stress

Plants are restricted to the germination site and exposed to variable temperatures. High temperature increases the fluidity of cytoplasmic membrane whereas low temperature makes the cell membrane rigid. A deviation in the temperature above or below the optimum range has a rippling effect on the growth and development of plants as temperature severely upsets the plant water relations, photosynthesis, flowering and fruit setting in temperate as well as tropical crops. Heat stress stands as a prominent abiotic stress, inducing substantial alterations in plant hormone levels and their corresponding responses. Heat stress raises the morbidity and mortality of plants and deteriorates their quality (Santos et al 2022; Haider et al 2022; Perrella et al 2022) and these changes become irreversible if the stress lasts for a long time. Plants adopt diverse mechanisms to withstand heat stress for example production and accumulation of osmolytes, enzymes, HSPs and ROS scavenging enzymes namely ascorbate peroxidase and catalase (Qu et al 2013). However, the majority of crops exhibited limited tolerance to extreme temperatures, including both heat stress and cold shock. Therefore, strategies to make agricultural production sustainable in changing climate need to be developed. Temperature plays an imperative role in regulating the metabolism and physiology of microbes. Microbes possess remarkable enzymatic capabilities that aid them in adapting to both low and high temperatures. These microorganisms have efficient mechanisms to safeguard their proteins, membranes, and nucleic acids, enabling them to thrive under such challenging conditions.

Interaction between Plant and PGPR under Heat Stress

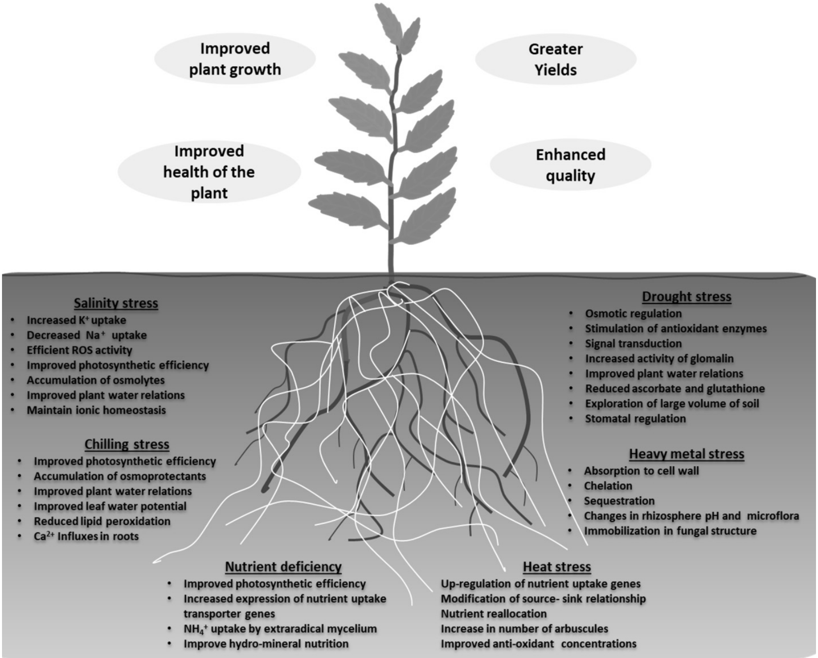

Figure 1. Plant-microbe interaction under heat stress.

Plants and microbes interact through various mechanisms such as phytohormones and siderophores production, gene expression, osmolytes accumulation, and volatile compounds (Figure 1). These interactions contribute to the antioxidant potential of the plants and compatible osmolytes (proline, glycine betaine, soluble sugars and trehalose) accumulation, which helps to improve the nutrient status of stressed plants (Shaffique et al 2022). PGPR is well-known to promote plant tolerance against heat stress through several important mechanisms including improved availability of nutrients, biological nitrogen fixation, P solubilization, K and Zn solubilization, phytohormones (IAA, abscisic acid, cytokinins, giberellins, brassinosteroids, jasmonates, production of ACC deaminase) production, generation of antioxidant compounds, reducing generation of ROS, activation of heat shock transcription factors, effective nutrient and water uptake and enhanced photosynthesis and increased trehalose biosynthesis and accumulation. Trehalose accumulation helps in stabilizing the cell proteins under heat stress.

Low Temperature Stress

Low-temperature stress is a severe problem that reduces plant performance by affecting the basic metabolism, balance of antioxidant-ROS, activity of macromolecules, cellular osmotic potential, destabilization of protein complexes, fluidity of cytoplasmic membrane (Pedranzani et al 2016). Several researchers have documented the potential of PGPR in combating cold stress in plants.

The colonization of PGPR in the rhizosphere can enhance a plant's ability to withstand low-temperature stress. Epiphytic bacteria possessing ice nucleation ability, such as *Pseudomonas syringae*, play a role in mitigating frost injuries in low-temperature-sensitive plants by preventing the formation of ice crystals that can damage the cytoplasmic membrane (Lindow and Brandl 2003). Certain low-temperature-tolerant PGPR strains, such as *Serratia marcescens* SRM (MTCC 8708) and *Pantoea dispersa* 1A, exhibit Plant Growth-Promoting (PGP) characteristics including phosphorus solubilization, IAA production, hydrogen cyanide (HCN) production, and siderophore production. Inoculation of wheat seedlings with these strains under chilling conditions has been shown to enhance nutrient acquisition and biomass production (Selvakumar et al 2007). Additionally, Barka et al. (2006) observed a decreased rate of biomass reduction and electrolyte leakage in grapevines upon inoculation with *Burkholderia phytofirmans* PsJN. Electrolyte leakage serves as an indicator of injury to the cytoplasmic membrane during cold treatment (4°C). These findings underscore the potential of PGPR inoculation in bolstering plant resilience to low temperature stress, thereby contributing to improved plant growth and survival under challenging environmental conditions. They also observed increased proline, starch, phenols, photosynthesis rates and starch deposition. Fernandez et al (2012) observed the grapevine surviving at low temperatures with the application of *Burkholderia phytofirmans* PsJN which helped in increasing photosynthesis and regulating metabolism of carbohydrates. Cold-tolerant *Rhizobium leguminosarum*-PR1 and *Pseudomonas* spp. acclimatized lentil to low temperature and improved its nutrient uptake, iron procurement and growth (Mishra et al 2011).

Heavy Metal Stress

Heavy metal stress has emerged as a significant threat to ecosystems worldwide due to intensive agricultural practices, industrialization, and anthropogenic activities leading to soil contamination. This contamination poses serious risks to both plant and human health. In polluted soils, root development and poor growth are primary limiting factors for successful crop production. Common effects include increased uptake of heavy metals and reduced rates of photosynthesis, impacting various physiological traits (Selvakumar et al 2012). Heavy metals are metallic elements with a density greater than 4 g/cm^3, characterized by their non-degradability and toxicity even at low concentrations (Ma et al 2016). They can damage soil texture and adversely affect crops, necessitating the removal and detoxification of heavy metals from soil to protect the environment. However, conventional methods for heavy metal removal are often costly and can have negative effects on soil structure (Glick 2010). Bioremediation, involving either plant (phytoremediation) or plant-associated microbes, has emerged as a sustainable and effective approach for heavy metal removal from soil. This method is cost-effective, environmentally friendly, and sustainable. Additionally, the inclusion of microbes enhances the efficacy of phytoremediation. Microorganisms, being sensitive to heavy metal stress, serve as good indicators of contamination (Chirakkara et al 2016).

Various microorganisms and plant-associated microbes, such as rhizobacteria, mycorrhiza, and firmicutes, have demonstrated the ability to thrive in the presence of heavy metals while enhancing plant growth and development under metal-stressed conditions (Table 1). These microbes employ diverse mechanisms for bioremediation, including metal impermeability, efflux, volatilization, metal complexation, exopolysaccharide sequestration, and enzymatic detoxification. Both living and dead microbial biomass have been utilized for heavy metal removal, with bioaccumulation by microbes proving to be an effective method for soil remediation. Studies have indicated that Proteobacteria, Actinobacteria, and Firmicutes effectively remove higher concentrations of metals such as Mn, As, and Pb from contaminated soil (Zhang et al 2015). AMF have been found to alleviate the harmful effects of Cd stress by reducing malondialdehyde and hydrogen peroxide levels (Hashem et al 2016). Researchers have identified several microorganisms capable of heavy metal removal, including *Klebsiella* sp., *Enterobacter* sp., *Micrococcus* sp. MU1, and *Pteris vittata* (Jing et al 2014; Prapagdee et al 2013). These findings highlight the diverse range of microbial species that contribute to heavy metal bioremediation, offering promising solutions for mitigating the impacts of heavy metal contamination in soils.

Alleviation of Abiotic Stress by Arbuscular Mycorrhizal Fungi (AMF)

The symbiotic associations of AMF with plants are a perfect example of mutualistic relationship where both the partners are mutually benefitting each other. The symbiosis is reported to be around 400 million years old. The fungal mycelium colonizes roots of more than 80% of the plant species forming a common mycorrhizal network (CMN) (Smith and Read 2010). AMF can revamp the properties of soil, make provisions for better nutrient uptake by plants, hence improve plant growth and development under normal and stressful conditions. Nowadays, AMF are of prime importance and can be used as bio-inoculants for sustainable crop production (Narwal et al 2018). The significantly higher soil organic biomass of AMF-inoculated soils due to higher extra-radical mycelium is a great way of carbon sequestration. The glycoproteins known as glomalin-related soil proteins (GRSP) maintain soil water content and are believed to bind nutrients and also heavy metals (Singh et al 2017). Application of AMF for improving plant growth in different ecosystems can significantly contribute to organic matter build-up in soil and also for boosting plant growth to augment crop yields in a sustainable way (Figure 2). Symbiotic association of higher plant roots and AMF is mainly known to improve resistance to the plant against water scarcity and drought conditions by several modifications in plant physiology and gene expression (Table 2). Alleviation of abiotic stresses by AMF colonization may be attributed to increased nutrient (especially P) and water uptake. AMF is a very important component of the plant-soil system. AMF symbiosis helps in nutrient exchange between soil and plants. It helps improve stress tolerance through nutrient and water uptake by extra radical hyphae, boosts gas exchange and water use efficiency, maintains plant hormonal status, improves soil structure by glomalin and regulates antioxidant system (Pedranzani et al 2016).

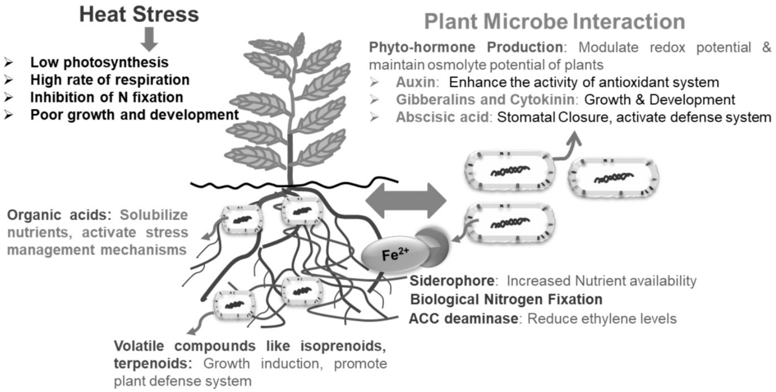

Fig 2. Mechanisms used by AMF to mitigate abiotic stress conditions in plants.

AMF colonization helps in lowering plasma membrane permeability and decreasing malondialdehyde content and soluble protein content in the leaf which stimulates the peroxidase, superoxide dismutases, and catalase activity resulting in better osmotic regulation and drought tolerance (Wu and Xia 2005). AMF application results in the osmotic regulation of plant by boosting levels of non-structural carbohydrates, K^+, Ca^{2+} and Mg^{2+} leading to the improvement of drought stress tolerance (Wu and Xia 2005). Porcel et al (2006) identified a gene encoding 14-3-3 protein from *Glomus intraradices* grown *in vitro* under drought conditions. These proteins play an important role in regulating signalling pathways and also as effector proteins in imparting safeguard to plants against drought stress. Ascorbate and glutathione have vital functions in imparting protection and maintaining metabolic functions of plants under drought conditions. Lower accumulation of these compounds in plants colonized by AMF results in higher root biomass, water content, nitrogen and potassium content (Marulanda et al 2007). Growth and development of the plants in saline soils is improved by *Glomus* spp. Inoculation resulting in increased phosphate and reduced Na^+ ion concentrations in shoots as compared to uninoculated control (Giri and Mukerji 2004). *Casuarina equisetifolia* seedlings inoculated with AMF could adapt better under flooding than non-inoculated seedlings which may be due to improved oxygen diffusion and ethanol removal through better development of adventitious roots, aerenchymatous tissue and hypertrophies lenticels on root and submerged stem (Grover et al 2011).

AMF inoculation results in improved photosynthetic characteristics, chlorophyll synthesis, water-use efficiency, plant-water status, and activity of catalase, super oxide dismutase, peroxidase *etc.* in plants grown under cold stress (Xian et al 2010). The formation of an extensive network of fungal hyphae and glomalin secretion improves the water and nutrient uptake, soil structure and stability of soil aggregates (Miransari 2016). AMF colonization enhances soil water uptake, thereby regulating stomatal aperture to achieve improved water use efficiency. It also helps to maintain cytokinin and auxin concentrations, boost stele tissue size, and promote the accumulation of osmolytes (Fan and Liu 2011). AM symbiosis alleviates injuries caused by saline conditions by regulating nutrient and water uptake, accumulation of organic solutes, maintaining high photosynthetic efficiency, enhanced protein synthesis, increasing root hydraulic conductivity, improved hormonal status of the plant and efficient ROS-scavenging activity. Under heat stress, antioxidant compounds such as polyphenols and ascorbic acid, activity of superoxide dismutase and ascorbate peroxidase are higher in AMF-inoculated plants (Maya and Matsubara 2013). Under low temperature stress, AM symbiosis helps in plant tolerance through chlorophyll synthesis, better water use efficiency, higher photosynthesis, accumulation of osmo-protectants such as soluble sugars, proteins and proline, enhanced antioxidant system, increased accumulation of flavonoids, phenolics and lignin and decrease in H_2O_2 accumulation (Chen et al 2013). In heavy metal-polluted soil, AM plants exhibit increased biomass and enhanced tolerance due to several mechanisms, including metal binding to chitin in the cell wall, internal chelation of metals within the fungus, binding of metals to metallothioneins within fungal or plant cells, sequestration of heavy metals *via* siderophores, containment of metals through compounds released by the fungus, immobilization of heavy metals on hyphae leading to intracellular sequestration, alterations in rhizosphere pH and microflora, resulting in reduced availability of heavy metals (Hossain et al 2012).

Table 2. Effect of AMF inoculation on plants under different stresses.

Crop	**Type of Stress**	**Microorganism Involved**	**Mechanism**	**Reference**
Pistachio (*Pistacia vera*)	Drought	*Glomus etunicatum*	ROS scavenging, higher root and shoot biomass	Abbaspour et al 2012
Pomegranate (*Punica granatum*)	Drought	*Rhizophagus intraradices*	Higher activity of superoxide dismutase and catalase in shoots	Bompadre et al 2014
Maize (*Zea mays*)	Drought	*Glomus intraradices*	Higher expression of two aquaporin genes (*GintAQPF1* and *GintAQPF2),* thus enhanced water uptake	Li et al 2013
Wheat (*Triticum aestivum*)	Drought	*Glomus mosseae, Gigaspora decipiens, Glomus fasciculatum*	Increased plant growth parameters, and total chlorophyll pigments	Pal and Pandey 2016
Poplar (*Populus* spp.)	Salinity	*Rhizophagus irregularis*	Enhanced water use efficiency, improved photosynthesis and higher biomass	Wu et al 2015
Lettuce (*Lactuca sativa*)	Salinity	*Glomus intraradices*	Lowered abscisic acid levels, improved plant growth	Jahromi et al 2008
Lettuce (*Lactuca sativa*)	Salinity	*Glomus intraradices*	Lowered abscisic acid levels, improved stomatal conductance and photosynthetic efficiency	Aroca et al 2013