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REVIEW ARTICLE

Role of microbes in alleviating abiotic stress in plants

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Abstract

The leading threat to agricultural productivity is the recurrent variations in environmental conditions. A battery of abiotic stresses namely flooding, salinity, temperature, drought, heavy metal toxicities, nutrient deficiencies and oxidative stress causes irreversible damage resulting in loss of plant's vigor and yield. The relationship between plants and microorganisms is a highly dynamic system. The plant microbiome consists of plant growth-promoting bacteria and fungi. In the last decade, many microbes that give hosts the ability to withstand abiotic stress have been characterized in detail. Their beneficial association with plants enables the plant to endure different stresses imposed on them thereby enhancing the plant's sustainability and productivity. For sustainable agriculture, it is very significant to comprehend microbiome-assisted mechanisms for mitigating abiotic stress. This review will shed light on the current knowledge about the roles of various microorganisms in mitigating against abiotic stresses. The understanding of these mechanisms will help to increase the yield of plants and meet the food demands of the expanding population.

Keywords

Abiotic stress, bacteria, fungi, mitigation, plant microbe interaction

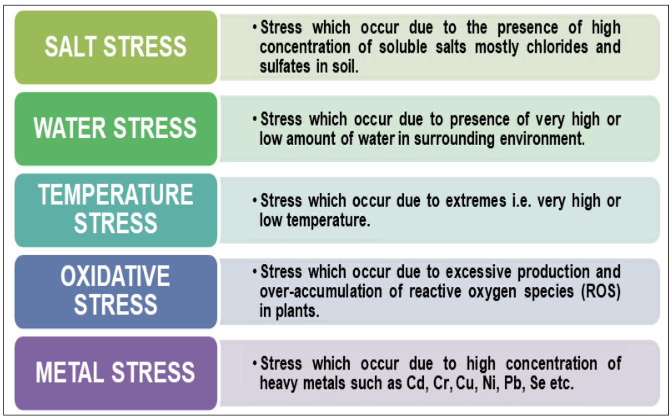
Introduction

A major threat faced by mankind today is global warming that is due to mindless anthropogenic activities in the last decade. Due to global warming it is expected that by 2050 the global temperature will rise by 2^{0}C (1). Climate change drives several extreme environmental events like drought, flood, disturbed rainfall patterns and an increase in pests that pose a significant threat to agriculture and crop productivity. According to a recent impact assessment study based on the crop simulation model Decision Support System for Agrotechnology Transfer (DSSATv4.6), it has been predicted that there would be a yield reduction of 15.2% in rice and 14.1% in wheat during the mid-century (2040-2069) (2). Scientists and breeders are continually faced with the task of preserving food security on a sustainable basis for the future generation.

Genetic engineering is the technology of developing new crop varieties with desired characteristics like high yield, nutritional enhancement, resistance to several abiotic and biotic stresses etc. through the insertion of a foreign gene of the same desirable characteristics (3). Using various conventional and unconventional techniques scientists have successfully developed several genetically modified (GM) plants with desired features (4). Using a variety of new tools, such as clustered regularly interspaced short palindromic repeats (CRISPRs), transcription activator-like effector nucleases (TALENs), zinc-finger nucleases (ZFNs) and plant genome editing has helped in the development of improved crops in novel ways (5). These new technologies have proved helpful in coping with various agricultural and environmental threats.

The fact that plants are rooted in one place makes them vulnerable to a wide variety of abiotic pressures. Changes in the climatic conditions that result in deviation from the homeostatic state can be defined as stress. Stress can broadly be of 2 types-biotic and abiotic. Biotic stress is a result of various living factors like viruses, bacteria, fungi, nematodes or insects that result in diseases (6). Abiotic stress results due to various non-living factors like salt, excess water or water deficit, low or high temperature, heavy metals (HMs) and ultraviolet radiations all of which adversely affect plants (Fig. 1) (7). Abiotic stress is the major factor that adversely affects agricultural yield (8). It has been reported that in India nearly 11 Mha area is affected by salinity and 16 Mha by water-logging (9).

The development of effective solutions for the control of abiotic stress is one of the critical global issues to maintain sufficient crop output in light of the extensive damage caused by abiotic stress. Various strategies developed for abiotic stress management include development of varieties tolerant to abiotic stress through breeding, resource management practices, generation of abiotic stress-resistant transgenic plants, shifting of crop calendars etc. (10). Although these approaches show promise, they are time-consuming, labor-intensive and expensive. Several studies have demonstrated the efficacy of using microorganisms to counteract the effects of abiotic stress (11). Inoculation of plants with microbes for mitigating abiotic stress has the advantage of being environmentally friendly, cost-effective and can be available in a shorter time (9).



SALT STRESS	• Stress which occur due to the presence of high concentration of soluble salts mostly chlorides and sulfates in soil.
WATER STRESS	• Stress which occur due to presence of very high or low amount of water in surrounding environment.
TEMPERATURE STRESS	• Stress which occur due to extremes i.e. very high or low temperature.
OXIDATIVE STRESS	• Stress which occur due to excessive production and over-accumulation of reactive oxygen species (ROS) in plants.
METAL STRESS	• Stress which occur due to high concentration of heavy metals such as Cd, Cr, Cu, Ni, Pb, Se etc.

Fig. 1. Major abiotic stresses that affect plants.

Soil is home to a diverse community of microorganisms that are collectively known as the microbiome. The microbiota has been shown to have a major role in the growth and development of plants. They help in efficient nutrient uptake, disease tolerance and abiotic stress response. The plant microbiome consists of plant growth-promoting fungi (PGPF) and bacteria (12). Micro-organisms that are present in the soil are mostly found around the root zone, i.e. rhizosphere of plants as it is rich in organic carbon provided by roots (13). The rhizobacteria are comprised of various bacterial species such as *Enterobacter, Bacillus, Pseudomonas, Arthrobacter*, *Azospirillum*, *Streptomyces* and *Azotobacter* (14). Plant growth-promoting rhizobacteria (PGPR) is a class of rhizobacteria shown to stimulate plant's growth by releasing phytohormones like auxin, gibberellins, abscisic acid (ABA) and cytokinin (15). Additionally, other compounds like siderophores, enzymes, antibiotics and organic acids have also been shown to be secreted by rhizobacteria that result in plant growth stimulation (16). They have critical roles in nutrient cycling and promotes plant growth by improving uptake of nutrient, secreting enzymes as well as organic compounds and inhibiting fungal pathogens (17). Many of the bacteria found in the rhizosphere also penetrate the root cortex and are thus called endophytic bacteria. The most commonly found species of endophytic bacteria are *Enterobacter, Bacillus*, *Serratia*, *Klebsiella*, *Pseudomonas* and *Streptomyces* (18).

Endophytic fungi also directly or indirectly help host plant species survive abiotic stress. The direct beneficial mechanism involves phytohormone production, nitrogen fixation, phosphate solubilization, siderophore production and anti-microbial metabolite production (19). The indirect beneficial mechanism involves the modification of the metabolic process of biocontrol, bioremediation and phytoremediation (20). Cosmopolitan fungal endophytes act as biostimulants to produce certain bioactive compounds, phytohormones, phosphate solubilization factors etc., to enhance root growth, seed germination and plant growth promotion (21). Ascomycetes species, *Fusarium* sp., *Cladosporium* sp., *Penicillium* sp., *Verticillium* sp. and *Aspergillus* sp. all live in *Panax ginseng* and secrete triterpenoid saponins and ginsenosides which enhance root growth and tolerance to biotic and abiotic stress (22). Agaricomycetes member like *Piriformospora indica* increases root proliferation brought on by indole-3-acetic acid (IAA) production, which in turn leads to higher nutrient uptake and ultimately, improved crop yield (23).

Plants also show symbiotic association with a group of fungi called arbuscular mycorrhizal fungi (AMF). In the AMF association, the fungal partner gets protection and photosynthates from plants while it confers the properties of abiotic stress tolerance and efficient nutrient uptake to plants (24). The AMF has been reported to impart tolerance to salinity stress, osmotic stress and water stress (25). Apart from AMF, various fungi have also been shown to be part of the microbiome such as *Trichoderma* which has been used traditionally in plants for accelerated growth and abiotic stress tolerance (26). *Rhizobium* also plays important role in ameliorating various abiotic stresses in plants by enhanced IAA production which leads to improved root growth and better nutrient uptake. In addition, *Rhizobium* also helps in exopolysaccharide production which helps in making a layer of moisture around roots resulting in the maintenance of the water potential gradient under water stress (27).

The plant-microbe interaction plays a crucial role in imparting abiotic stress tolerance. The underlying mechanism may be varied such as the release of plant growth-promoting substances, up-regulation of novel genes, triggering osmotic responses etc. (11). In this paper, we review the progress achieved in the area of alleviation of several abiotic stresses like HMs, drought, temperature extremes and salinity by plant microbiome and the underlying mechanism. Genes isolated from microorganisms have also been transformed into plants for conferring abiotic stress tolerance, such GM plants have also been discussed.

Abiotic stress: Its effects and responses in plants

Abiotic stress is a kind of environmental stress that restricts plant metabolism and development. Abiotic stresses can be categorized into atmosphere-induced or edaphic. Further growth, metabolism and development of both aboveground and belowground plant parts can be affected by these stresses (28). Abiotic stress influences the morphology, physiology, anatomy and behavior of plant species with respect to their growth, development and have a significant negative effect on crop yields (7). Consequently, the issue of global food security is becoming very serious. Plants have complex, dynamic, reversible and irreversible responses to abiotic stress. Abiotic stress causes extensive alterations in cellular processes and affects many parameters of plant's physiology.

The processes of adaptation, acclimation and speciation as well as the activation of numerous responses involving physiological, morphological and anatomical changes, alterations of the membrane and cell wall, metabolic crosstalk with numerous molecular pathways and intricate gene interactions allow plants to sense and respond to abiotic stresses (29, 30). Over the last several decades, scientists have worked to dissect the complex molecular interactions that occur in plants in response to abiotic stresses (30).

Stresses affect plant dispersion, growth and development and agricultural production. Sensing abiotic stress initiates a multifaceted stress-specific signaling cascade, including activation of ion channels and kinase cascades, production of reactive oxygen species (ROS), flavonoids and phenolic acids accumulation and enhanced synthesis of antioxidants, osmolytes and hormones (31) which are involved in processes like signal detection, transduction, transcription, translation and post-translational protein modification. These signals trigger the activation of stress-specific genes that contribute to proper defense and activate transcription factors (TFs; 17). This information may be used to improve crop output and agricultural sustainability via chemical, genetic and microbiological techniques (30). The following section discusses the impact of various abiotic stresses on plants and their responses.

Salinity stress

The second major limiting factor that has a significant impact on agricultural yield is hypersalinity or deficiency. Salinity is a common mineral toxicity factor that is thought to affect 10% of the earth's land surface, especially in irrigated areas. By 2050, approximately 50% of the land used for agriculture is expected to be destroyed if rising salinity is not addressed (32). Salinity limits water uptake by reducing plants' water-absorbing capacity by lowering the water potential of soil. Secondly, it interferes with the plant's process of absorbing nutrients, leading to an imbalance of nutrients in plants (33). Salinity hinders plant growth and reduces agricultural yield worldwide. Salinity impacts seed germination, plant development, photosynthetic efficiency, ionic imbalance, and osmotic condition in plants, which has serious consequences for the plants' morphology, biomass and metabolic activities, eventually resulting in plant destruction (34, 35). Long-term salt stress elevates the concentration of ions, causing ion cytotoxicity, which is extremely harmful to plants (36).

Soil with high salt concentrations is not only harmful to plants because it prevents them from getting the water and nutrients they need, but also because it hinders the root's ability to absorb water from the soil. Prolonged salinity leads to ionic stress, which results in a reduction in the photosynthetic area (37). The structural phenotypes of plants under excessive salt stress include yellow spots on the leaf margins, reduced shoot, root and stem length, decreased bud formation, as well as diminished fruit colour and flavour. These effects slows the growth and lowers the yield (38).

Plants respond to high salinity by compartmentalising ions away from the cytoplasm of physiologically active cells or by oozing ions from roots in order to protect vulnerable plant tissues from the high salinity zone (39). Increased salt concentration can prevent plants from absorbing water through their roots, causing drought stress. It can also affect various physiological processes, such as photosynthesis, necrosis of leaves, cellular toxicity, osmotic stress, oxidative stress and hormonal imbalance. Finally, it can prevent plants from absorbing essential nutrients, ultimately causing plant death (40).

The ability to tolerate salt is a complex trait that depends on the coordinated action of numerous genes that carry out several tasks, including ion sequestration, metabolic and osmotic adjustment, and antioxidant defense (41). Plants have developed many adaptive processes to overcome salt stress like salt exclusion, intracellular compartmentalization, synthesis of osmoprotectants like proline, sugars, glycine, amino acids, betaine and compatible solutes, amendment of membrane structure, modulation of hormones, induction of antioxidant enzymes such as peroxidase (POD), ascorbate peroxidase (APX), glutathione reductase (GR), catalase (CAT), superoxide dismutase (SOD) and nitric oxide generation (40) and synthesis of some crucial non-enzymatic antioxidants namely ascorbate, carotenoids and tocopherol (41).

Drought stress

Drought stress is one of the main environmental factors contributing to reduced agricultural productivity. Different studies on maize, sorghum, wheat and cotton have suggested that drought severely affects the yield of these crop plants (42, 43). This significant environmental stress is caused by changes in temperature, light intensity and inadequate rainfall. Modifications of their morphological, biochemical, physiological and molecular characteristics, reduce plants' ability to photosynthesize. Plants have developed a range of complex species-specific resistance and adaptation mechanisms in response to water scarcity (44). Among the typical signs of drought stress in plants are the rolling of leaves, stunting of plants, yellowing of foliage, blistering of leaves and persistent wilting (45). Drought stress affects plant's growth, water uptake and photosynthetic capacity as a result of a reduction in leaf water potential, alteration in cell wall properties and changes in stomatal closure which limit the CO_2 uptake and increase the photoinhibition. Water stress also alters a variety of physiological reactions, including a reduction in transpiration, chlorophyll content and Rubisco efficiency, increase oxidative stress, suppresses root growth, delays flowering and fruiting and affects seed size, yield and productivity (44). To combat water stress plants develop numerous mechanisms, including increased activity of SOD and enhanced accumulation of suitable solutes like sugars, proline, betaines, polyamines, quaternary ammonium compounds, polyhydric alcohols and amino acids. The osmotic adjustment shields proteins, enzymes, organelles and membranes from oxidative damage at the cellular level, enabling plants to withstand damage brought on by drought (46).

Temperature stress

Global warming and climate change have increased the frequency and severity of heat waves, freezing, temperature patterns and other abiotic stresses such as salinity, drought and flooding (47). Plants display both long-term and short-term effects in response to temperature stress (heat or cold). Short-term effects include altered leaf orientation, increased transpiration and changes in membrane lipid, while long-term effects alter morphological and phenological adaptations (48). The temperature prevailing around plants is a significant factor for determining how fast they grow and develop since every plant has a specific temperature range ranging from a minimum, optimum and maximum. Heat stress affects plant growth and development by disrupting proteins, membranes and cytoskeleton structures. Temperature stress affects various stages of plant development. Reactive oxygen species are produced in excess as a result of heat stress, which leads to oxidative stress (49). High temperature also affects other plant processes like seed germination, respiration, photosynthesis, membrane permeability, growth, reproduction and yield (50). Plants' responses to heat stress include fluctuations in phytohormones, primary as well as secondary metabolite levels and increased expression of heat shock and related proteins. Increased temperature as a result of global warming can hinder the growth of the plant and their development or kill crops in extreme cases. Heat stress impacts photochemical reactions, chloroplast biosynthesis, photosynthesis, electron transport and CO_2 assimilation. According to recent research, during heat stress, chloroplasts activate nuclear, heat-responsive genes (51).

In addition to heat stress, plants also experience chilling stress, when the temperature drops from 15°C to 0°C, it is a type of temperature stress that is non-freezing and has a significant impact on cell physiology (52). Chilling stress causes biological membranes to become rigid, stabilize nucleic acids, produce ROS and inhibit photosynthesis, ultimately leading to cell death. The cold-hardening process involves the up-regulation of metabolic processes that impart tolerance in plants, leading to the production of compatible solutes (such as sugar), changes in the composition of the membrane and increases the production of dehydrin-like proteins (48).

Heavy metal stress

Heavy metal comprises both biologically essential elements such as copper (Cu), manganese (Mn), cobalt (Co), chromium (Cr) and zinc (Zn); required at low concentration and non-essential elements like cadmium (Cd), lead (Pb) and mercury (Hg), which are toxic to plants as well as humans (53). The growing urbanization and industrialization are widely recognized to have a considerable impact on HM pollution. As a consequence, anthropogenic actions like smelting, mining and agricultural management are regarded as significant contributors to HM contamination in the environment. Heavy metal pollution in agricultural soil is also caused by a variety of anthropogenic activities, such as the prolonged application of phosphate fertilizer, the use of sewage sludge, industrial water, smelter dust etc. (54). However, some factors like volume and surface area of the root and root-specific length in the root zone, also significantly results in the building up of HMs in various plant species (55).

High levels of HMs in the soil have an impact on plant development and growth, reduce enzyme activity, decrease photosynthetic activities and also affect mineral nutrition. A plant's immediate response to HM stress includes the reduction or prevention of the uptake of these metals into root cells. Other responses include chelation, trafficking, transport and sequestration of these metals into the vacuole. Plants synthesize proteins, signalling molecules, hormones and heat shock proteins and also activate mechanisms for oxidative stress defense (56). The plant-endophyte interaction causes plants to protect themselves from adverse environmental situations like HM exposure and drought stress (57). Plants have developed various defense mechanisms to safeguard their physiological systems from HM stress, including detoxification, compartmentalization and sequestering of metals inside vacuoles, changing the pH in the rhizosphere, binding metallothionein and stimulating various antioxidant enzymes (58).

Heavy metals may inhibit root growth, which could change water balance and nutrient absorption, affect their transportation to above-ground plant parts, negatively impact shoot growth, and ultimately lead to a reduction in biomass accumulation (59). The finding also demonstrate that multiple HMs stress increased root oxygen leakage, increased root activity and decreased root porosity in *Kandelia obovate* (60).

Although some metals, like Zn, Cu, Co and Mn, are necessary for various metabolic and developmental pathways at low concentrations, soils with elevated concentrations above threshold levels adversely affect plant physiology, metabolomics and biochemical rprocesses which results in stunted growth, biomass and yield (61). Lead hinders seed germination, development of seedlings and roots, transpiration, cell division and chlorophyll synthesis in plants. It also alters the permeability of cell membranes and causes DNA damage by increasing ROS production, lipid peroxidation and inhibition of ATP synthesis (62). Cadmium even at low concentrations alters enzyme activities, such as those involved in the C3 cycle, phosphorus (P) and carbohydrate metabolism and CO_2 fixation. This can lead to stunted growth, leaf epinasty, chlorosis, changes in chloroplast structure and inhibition of photosynthesis (63). The excess of Fe^{2+} results in the production of free radicals, which permanently alter the cellular structure and harm membranes, proteins, and DNA. Although iron toxicity is uncommon, some plants do release acids from their roots, lowering the pH of the soil. These plants are toxic if they absorb too much iron. Cobalt toxicity results in reduced plant sugar, protein and amino acid content as well as reduced leaf area, shoot and root length. It also results in decreased chlorophyll content and activity of the antioxidant enzyme (64).

Plant defense against abiotic stresses

An array of abiotic stresses like HM, cold, heat, salinity etc. have adversely affected the growth, development and yield of plants. To combat this, plants have developed a range of mechanisms that help them to survive under harsh environmental conditions (65). Abiotic stress conditions trigger a complex set of defense responses in plants at molecular and cellular levels. Plants have numerous signalling pathways which help them withstand changing environmental conditions. There are various receptors that perceive the abiotic stress signals such as receptors for ROS, G-protein-coupled receptors, histidine kinases, receptor-like kinases etc. (66). Perception of signals by these receptors triggers a cascade of pathways which includes ROS production, changes in gene expression, mitogen-activated protein kinases (MAPK) based phosphorylation resulting in abiotic stress response (67, 68). Respiratory burst oxidase homolog (RBOH) proteins are one of the major proteins involved in the ROS-mediated signalling pathway. Respiratory burst oxidase homolog proteins are NADPH oxidases present on the plasma membrane and are found to be activated by phosphorylation and binding of calcium (Ca^{2+}) ions or other compounds (69).

PAMP/MAPM triggered immunity (PTI) is the first general response known to be triggered against biotic as well as abiotic stresses in plants. Pattern recognition receptors (PRRs) located on the surface perceive the extracellular signals which trigger the phosphorylation of RBOH (70). This activates NADPH oxidase phosphorylation which leads to ROS production in a calcium-dependent and independent manner. The Ca^{2+} signals are perceived by calcium-dependent protein kinases (CDPK). These MAPK and calcium-dependent signaling pathways are known to be involved in animals, plants as well as yeast. Signals perceived in the nucleus as a result of Ca^{2+} and MAPK phosphorylation activate multiple TFs (71, 72).

Several hormone [salicylic acid (SA), cytokinins, ABA, ethylene (ET), auxin, brassinosteroids, gibberellins, strigolactones and jasmonic acid (JA)] signaling pathways are known to be involved in abiotic stress response (66, 73, 74). The cross-talk between ROS production and hormone signaling pathways results in numerous physiological, metabolic and molecular changes resulting in the survival of plants under abiotic stress conditions (66).

The role of the plant microbiome

Plants are surrounded by different microbial populations that are specific to each plant part like rhizosphere (75), phyllosphere (76), endosphere (77) and spermosphere. The rhizosphere is the most important habitat due to its enormous potential for plant vigor and nutrition (78). The rhizosphere releases approximately 5% to 21% of the carbon that plants fix during photosynthesis. The phyllosphere is comparatively nutrient deficient and can tolerate extreme temperatures and humidity. Microorganisms of the rhizosphere and phyllosphere present near the surface or over the plants behave as epiphytes, while microorganisms that inhabit the plant tissues, either in the stem, leaves, or roots are called endophytes (79). The spermosphere is the area immediately around seeds and it is here that interactions between bacterial communities found in seeds, germinated seeds and soil take place. By stimulating the plant's physiological defense against oxidative damage, beneficial microorganisms can also improve seed germination under conditions of unfavourable temperature, salt stress or osmotic stress (80, 81). Eukaryotes, like fungi, algae, protozoa and nematodes are omnipresent in these regions and are significant symbionts or plant pathogens. Microbes associated with plants occupy a significant position in global biogeochemical cycles (82).

The microbial community inhabiting the rhizosphere differs from those found in other parts of the soil, mainly because they are immediately affected by the accumulation of root exudates and have easy access to nutrients, which increases microbial biomass. Root exudates are important in structuring the rhizosphere microbiome (83). The root exudates contain lipids, carbohydrates, organic acids, proteins, phenolic compounds and other biological components (84). The released mucilage also contains plant cell wall polymers mainly cellulose and pectin (85). A microbial community that is present over leaves is not uniform all-over but is impacted by different leaf features such as veins, midrib, hairs and stomata. The surface of the leaf contains microbes up to 10^7 per cm^2 (86). The phyllosphere is more diverse than the rhizosphere due to variations in temperature, radiation and moisture that affect microbial habitats. The phyllosphere region is occupied by fungi, bacteria, algae and to a lesser extent protozoa and nematodes (87). Endophytic bacteria have not been found to exist in active cells; instead, they have been found to dwell mostly in the intercellular apoplast and dead or dying cells. They are present in the xylem vessels; from there they can move from the plant's roots to the various aerial portions of the plant. By expressing cell walldegrading enzymes, the endophytic bacteria initially infiltrate the host through the lateral root junction (88). Primarily, endophytes defend plants from pathogenic infections and promote the growth of plant.

To mitigate the deleterious effects of abiotic stress on plant growth, microorganisms interact with plants through biochemical and molecular processes. Several soil -borne beneficial microorganisms such as PGPF and PGPR that secrete plant growth-enhancing hormones, e.g. auxin, provide nourishment to the host and defense against several biotic and abiotic stresses (89). *Rhizobia* sp. and AMF are examples of typical symbiotic bacteria that exchange plant photosynthates for the fixation of nitrogen, solubilization and mobilization of phosphates and nourishment (90). Apart from nutrition supply to the host, PGPR and PGPF may also prime the immune system thereby preventing direct immunological activation and also enhance defense responses against pathogens even in tissues away from the site (91). Furthermore, PGPR and PGPF activate induced systemic resistance (ISR) and mycorrhizal-induced resistance (MIR) (92) by up/down-regulating different phytohormonal pathways (93).

Mycorrhiza is the result of the mutual beneficial interaction between fungi and the roots of higher plants. In the AMF, the fungus can be found inside the root as intraradical hyphae, vesicles and arbuscules, or it can be found outside the root in the soil as extramatricular chlamydospores and extra-radical hyphae. The AMF genera that are frequently found are *Entrophospora, Acaulospora*, *Gigaspora, Glomus* and *Scutellospora*. They are obligate symbionts. Mycorrhizal plants increased plant development in poor to moderate fertile soil by enhancing nutrient absorption, particularly of Pb, P, Cu and Zn. These associations also have other beneficial effects like endogenous hormone production, biological control of root infections and resistance to water stress (94). Arbuscular mycorrhizal fungal hyphae help in improving soil properties by increasing the soil water holding capacity (95) and also increase the root’s ability to absorb water by strengthening the root architecture (96). Arbuscular mycorrhizal fungi also regulates numerous physiological functions of plant-such as leaf water potential, nutrient uptake, stomatal conductance, transpiration rate, photosynthesis and synthesis of antioxidative enzymes and growth-promoting hormones (25). According to several reports, AMF stimulate the expression of the ammonium transporters in plants to enhance ammonium absorption. LeAMT4 and LeAMT5 of tomato, SbAMT3.1 of sorghum, ZmAMT3.1 of maize and LjAMT2;2 of *Lotus japonicus* are some of the AMF-induced ammonium transporters characterized in plants (97-100).

Plant-growth-promoting bacterial endophytes (PGPBEs) enhance plant growth via three different interconnected systems such as biofertilization, biocontrol and phytostimulation (101). Phytostimulation is the process that enhances plant growth by releasing phytohormones (101). The most important example of phytostimulation is the lowering of the concentration of the plant hormone, ET by the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase. Production of ACC deaminase enzyme may reduce the plant ET levels to alleviate abiotic stress, as enhanced ET levels inhibit DNA synthesis, cell division, shoot and root growth (102). The production of other plant hormones like IAA, ABA and jasmonates by microbes also results in better plant development (103).

The area around a plant's root is also known to be occupied by PGPF, which improves nutrient uptake and helps the plant withstand biotic and abiotic challenges. The 4 most significant PGPF are *Phoma*, *Fusarium*, *Trichoderma* and *Penicillium*. Presence of phosphate-solubilizing fungi *Fusarium*, *Penicillium* and *Aspergillus* in soil have been shown to increase P bioavailability in plants (104).

Biofertilization is the mechanism by which the growth of a plant is increased by the improved bioavailability of major nutrients to the host (105). Several plant growth promoting bacteria (PGPB) have been reported because of their capacity to fix nitrogen including *Azospirillum* sp. (106), *Pantoea agglomerans* (107) and *Azoarcus* sp. (108). Some PGPB (*Achromobacter xiloxidans* and *Bacillus pumilus*) have also been shown to be involved in increasing P solubilization (109). Safeguarding plants from phytopathogens is known as biocontrol. Various mechanisms known to be involved are the production of siderophores or antibiotics. Siderophores like SA and pyochelin have a chelating capacity and are indirectly involved in controlling the disease by competing with phytopathogens for trace metals (110). Several antimicrobial metabolites are released by PGPBEs, such as 2,4-diacetyl phloroglucinol (DAPG) which inhibits plant disease. Several rhizobacteria such as *Staphylococcus epidermidis*, *Burkholderia cepacia* and strains of the *Bacillus subtilis* group enhance the development of plants by releasing volatile organic compounds (VOCs) (111). Plant defense mechanisms being activated via ISR by some non-pathogenic rhizobacteria is another strategy to reduce the pathogenic activity of microorganisms. It is known that flagella, lipopolysaccharides, siderophores, VOCs and several other bacterial components can also activate the non-pathogenic rhizobacteria-mediated ISR signalling pathway (112).

Various strains of PGPR secrete VOCs, primary and secondary metabolites namely phenylpropanoids, terpenes and alkaloids which help in mitigating abiotic stress (28, 113). The secondary metabolites synthesis also significantly affect the productivity and plant growth (114). To establish a symbiotic relationship, secondary metabolites induce chemo-attraction of rhizobia and fungus to the roots (115). Root colonization with fungus enhances the activity of the genes responsible for the synthesis of secondary metabolites, increasing the niches and number of contact sites available to the colonizing hyphae (116). Some of the other secondary metabolites that microorganisms employ to scavange ROS and mitigate abiotic stress comprise phytoalexins, flavonoids, lignin precursors and carotenoids (117).

Different approaches used to study plant-microbe interactions

The plant-microbe interaction is very complicated and forms an intertwined system. To boost agricultural yield, it is critical to understand the stress-mitigating mechanisms.

Different molecular, biochemical and physiological studies are helping in dissecting this system. Multi-omics approaches are also emerging as promising techniques to elucidate the changes in the plant at the molecular level during the plant-microbe interaction (118, 119) (Fig. 2). Genomic studies of both the plant and microbe will help us to understand the function of various genes that are responsible for the interaction and also genes which help in assuaging the abiotic stress (120). Transcriptome studies involve the identification of unique transcripts important for plant-microbe interactions. Microarray technology and next-generation RNA sequencing have been exploited to generate enormous information about different stress-specific genes and miRNA at the transcriptome level (121, 122). Proteomics technology plays an important role in elucidating the presence of different proteins in microbes and plants, the protein-protein interaction, proteins involved in stress mitigation and proteins involved in different physiological pathways or networks up-regulated during host-microbe interactions for alleviating stress (123).

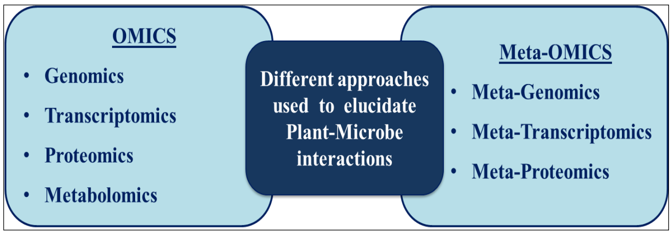


Fig. 2. OMICS strategies employed to explicate plant-microbe interactions.

Also, meta-omics strategies like metagenomics, metatranscriptomics and metaproteomics have unlocked new ways to explore diverse microbes under different environmental conditions and how they interact with plants. Metagenomics involves the characterization of genetic material isolated from the microbial habitat. Metagenomic studies provide an understanding of the composition, habitat and ecology of plant-associated microbes and the richness of stress-related genes. The availability of next-generation sequencing (NGS) technology along with metagenomics has further enhanced the speed and efficiency of the identification of microbial composition, function and diversity (124-126). Using metagenomic studies, the composition of drought-tolerant and resistant wheat seed microbiomes was also delineated (127).

Metatrancriptomics studies can also help in the identification of different microbial species and metabolic pathways under diverse environments (128, 129). Metaproteomics and secretomics studies have also helped in the functional characterization of microbial populations associated with plants (123). Metaproteomics can also be used to reveal the structure, interactions and regulation of microbial populations under different stress conditions (130).

Metabolomics or metabolic profiling employing gas chromatography linked with mass spectroscopy (GCMS) and high-performance liquid chromatography (HPLC) will aid in the identification and quantification of metabolites. Live cell imaging, confocal, fluorescence microscopy scanning and transmission electron and atomic force microscopy techniques have also been used to give a snapshot of the plant cell wall composition during plant-microbe interaction (131). Different mutant studies, gene silencing strategies using RNAi constructs, gene editing, metabolite profiling and proteomics studies have also revealed a lot of information about how microbes mitigate abiotic stress in plants (126, 132).

All of these methods will contribute to our understanding of the PGPR genome, proteome, transcriptome and metabolome, ultimately assisting in the improvement of PGPR strains. These altered PGPRs can subsequently be used to efficiently promote plant growth in a variety of environments (133). Data acquired from these methods can also be utilized to build integrative databases that will aid researchers in identifying new compounds that can be targeted to boost agricultural productivity (120).

Mitigation of different abiotic stresses by the plant microbiome

To withstand the imposed stress, plants have developed various adaptation strategies (Fig. 3). Microbes have a very dynamic function in developing plant tolerance to abiotic stress during plant-microbe interactions. This section will provide light on the many mechanisms employed by microbes to bestow abiotic stress tolerance to plants.

Microorganism-mediated salt resistance in plants

Salinity or salt stress is among the most important abiotic stress that limits seed germination thereby decreasing

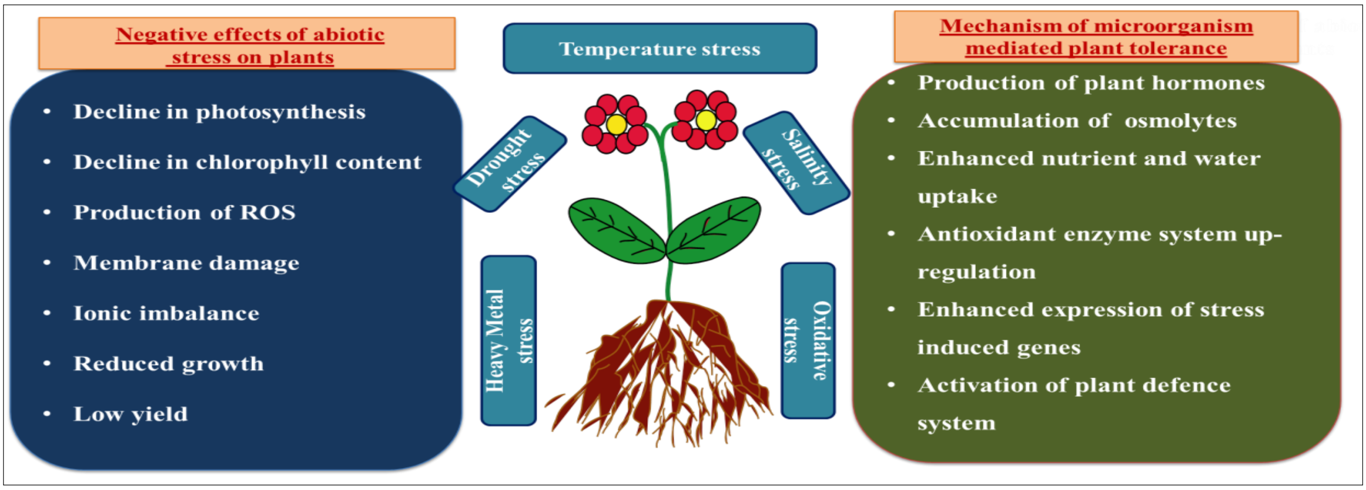


Fig. 3. Impact of abiotic stress on plants and microbial mechanisms underlying plant tolerance.

crop plant productivity in semi-arid and arid areas. Salt in the soil (edaphic stress) and the water used for irrigation has a detrimental effect on cultivable land, which has a significant influence on the growth and development of plants (134). According to the Food and Agricultural Organization (FAO), salinity can cause a significant loss of cultivated land, if proper measures are not taken (https://www.fao.org/global-soil-partnership/areas-of-work/soil-salinity/en/).

Salinity alters the physiological characteristics of cells, increases their osmotic potential, decreases microbial biomass as well as activity and alters the composition of microbial communities (135). To deal with salinity stress, PGPR employs various strategies like maintenance of ion homeostasis, accretion of different osmolytes and ROS scavenging enzymes and synthesis of different hormones and secondary metabolite (136). Plant growth-promoting microorganisms and AMF have also been demonstrated to elicit salt tolerance in many plants (137-140). Plant growth hormones or phytohormones are chemical messengers, which play a very crucial role in a plant's growth and development. One such phytohormone, auxin (indole acetic acid; IAA) plays a very important part in regulating root growth. Conversely, higher levels of auxin inhibit the growth of the root. According to previous reports, most of the rhizospheric bacteria have been shown to synthesize IAA (141, 142). *Enterobacter* sp. EJ01 enhances the fresh weight, height and dry weight of tomato and *Arabidopsis* plants exposed to high salinity conditions (143). Under salt stress conditions, wheat plants exposed to auxin-producing *Pseudomonas fluorescens* Ms-01 S3 displayed increased plant height, weight, proline accretion and antioxidant enzyme (POD and APX) activities (144). Recently auxin producing rhizobacterial strains *Bacillus mojavensis* S1 and *P. fluorescens* S3 have been demonstrated to reduce the effects of salt stress in barley (Rihane cultivar) plants by increasing nutrient and water uptake and stimulating the development of roots (145).

Another phytohormone, ET plays a significant role when the plants are subjected to any form of stress. The word "stress ethylene" has been coined to represent the raised levels of ET during stress. It is reported that elevated levels of ET adversely affect root growth (146). Rhizobacteria with ACC deaminase activity confer salt tolerance to many plants (147, 148). Enzyme ACC deaminase converts the precursor molecule of ET, ACC to ammonia and α-ketobutyrate. Plant growth-promoting rhizobacteria *Herbaspirillum* sp. strain GW103 having ACC deaminase activity conferred salt tolerance to *Brassica rapa* (Chinese cabbage) by enhancing K^+/Na^+ ratios in the root (149). Another bacterium *Enterobacter* sp. P23 enhanced the growth of rice seedlings exposed to salt stress by declining stress-induced ethylene and antioxidant enzyme levels (150). Enzyme ACC deaminase secreting PGPR ameliorated salt stress in *Phaseolus vulgaris*, *Solanum lycopersicum* and *Triticum aestivum* plants (151-153). Plant growth-promoting rhizobacteria namely *Bacillus marisflavi* and *Bacillus cereus* lessened the effects of salt stress in *Pisum sativum* (pea) plants by enhancing biomass, chlorophyll, flavonoids, sugars and antioxidant enzyme levels (154).

It is also shown that the higher salt level inhibits nitrogen fixation and nodulation in the symbiotic system like *Rhizobium* and legumes. Co-inoculation of PGPR and rhizobium improved salt tolerance in legume plants (155). *Glycyrrhiza uralensis* plants co-incubated with *Mesorhizobium* sp. strain NWXJ19 and *Pseudomonas extremorientalis* TSAU20 displayed improved nodulation, nitrogen content and growth under salinity stress environment (156). Similarly, co-incubation of *Rhizobium* and *Azotobacter* ameliorated salt stress effects by improving growth characteristics, nutrient absorption and productivity of *Cicer arietinum* plants (157). *Medicago truncatula* plants incubated with *Rhizobium meliloti* exhibited enhanced salt tolerance by increasing the synthesis of antioxidant enzymes and compatible solutes (158). *Rhizobium* sp. and *Hydrogenophaga* sp. when co-inoculated with *Bradyrhizobium japonicum* conferred salt tolerance to soybean by increasing N assimilation and K^+/Na^+ ratios (159).

Several PGPR have been shown to stimulate the growth of *Vicia faba*, *T. aestivum* and *Hordeum vulgare* plants exposed to salt stress conditions (160-162). *Capsicum annum* (pepper) plants incubated with rhizobacteria *Brevibacterium iodinum* KNUC7183 and *Rhizobium massiliae* KNUC7586 displayed enhanced antioxidant enzyme activities and altered proline and sugar levels under salinity stress (163). *Phaseolus mungo* plants challenged with halotolerant PGPR exhibited better plant growth, chlorophyll levels, yield and a decline in electrolyte leakage under salinity conditions (164). Similarly, salt-stressed *Medicago sativa* (alfalfa) plants incubated with *Pseudomonas* sp., *Hartmannibacter diazotrophicus* and other halotolerant PGPB showed improved growth performance and enhanced salt tolerance (165, 166). *Pseudomonas* PS01 bacteria conferred salt tolerance to *Arabidopsis thaliana* plants exposed to salt stress (167). Three varieties of rice namely Putra-1 (moderately tolerant), MR297 (susceptible) and BRRI dha67 (tolerant) when exposed to *Bacillus tequilensis* and *Bacillus aryabhattai* bacterial strains exhibited improved photosynthesis, stomatal conductance and transpiration resulting in higher yield (168). *Bacillus licheniformis* and *Pseudomonas plecoglossicida* rhizobacteria (shown to form biofilms, produce IAA and exhibit ACC deaminase activity) conferred salt tolerance to sunflower plants by improving their growth performance and enhancing the synthesis of enzymes with antioxidant activity (169). In another report, salt tolerant wheat variety AaS-11 incubated with a consortium of salt-tolerant PGPR displayed better growth and production under salinity stress (170). *Brevibacterium frigoritolerans* when co-inoculated with *Bacillus velezensis* and *Bacillus thuringiensis* stimulated the growth of wheat plants subjected to salt stress (171). Plant growth-promoting rhizobacteria *Acinetobacter bereziniae*, *Enterobacter ludwigii* and *Alcaligenes faecalis* also ameliorated salt stress in *P. sativum* plants by reducing H_2O_2 levels and leakage of electrolytes and increasing growth and yield (172).

A plant root inhabiting endophytic fungus *P. indica* conferred salt tolerance to barley plants which led to improved antioxidant enzyme activity and higher yield (173). *Piriformospora indica* enhanced growth and alleviated stress in *A. thaliana*, *Aloe vera* and *Lycopersicon esculentum* plants (174-176). A salt-tolerant endophytic species of *Fusarium* (extracted from Pokkali rice) stimulated the growth of IR-64 variety of rice under saline conditions by improving the physiological characteristics. Transcriptome analysis of plants inhabited with the endophyte showed activation of genes associated with stress tolerance (abiotic as well as biotic), signal perception and transduction, TFs etc. (177). Another root endophytic fungus *Serendipita indica* promoted the growth of *H. vulgare* plants exposed to salt stress by regulating photosynthesis and proteins important in carbohydrate metabolism (178).

Plant species also interact positively with AMF, a component of the plant microbiome. Arbuscular mycorrhizal fungi also alleviates salt stress by altering the membrane structure, accumulating osmolytes for better osmotic adjustment, increasing water and nutrient (Ca, Mg, N and P) uptake, photosynthetic efficacy, nitrogen fixation, sustaining the ratio of K^+ and Na^+, inducing the activity of antioxidant enzymes, and at molecular level up-regulating the expression of certain genes important for conferring salt tolerance (179). Reports also suggest a difference in the endogenous concentration of plant growth hormones during salt stress. Salicylic acid and ABA have been demonstrated to assist in conferring salt tolerance response (180). Arbuscular mycorrhizal fungi mixture alleviated salt stress in cowpea (*Vigna unguiculata*) and lupine (*Lupinus termis)* by inducing the activity of antioxidant enzymes, increasing proline synthesis thereby influencing osmoregulation and also increasing the uptake of nutrients (181, 182). In *Panicum turgidum*, AMF altered the osmoregulation and antioxidant and photosynthetic pathways for eliciting salt resistance (183).

Inoculation with *Glomus deserticola* also improved salt resistance in *Ocimum basilicum*, by increasing chlorophyll content, photosynthetic efficiency and water uptake (184). Colonization with AMF also mitigated the negative consequences of salt stress in *M. sativa, Sorghum bicolor* and *Oryza sativa* (Bangladeshi) plants (185-187). *Eucalyptus* seedlings inoculated with AMF species of *Glomus* and *Gigaspora* led to enhanced chlorophyll (50%), decreased leaf proline content (20%) and 3-6 fold increased K^+/Na^+ ratios when compared with non-inoculated plants exposed to salt stress environment (188). Improved salt stress tolerance was seen in *Gleditsia sinensis* plants when incubated with AMF as indicated by increased stomatal conductance of leaf, antioxidant enzyme activities, P/N ratio and decreased malondialdehyde (MDA) content (189).

A combination of AMF and bacteria has also been shown to mitigate the salt-induced negative effects. Dual inoculation of Mung bean (*Vigna radiata*) with AMF *Glomus mosseae* and *Acaulospora laevis* along with bacteria *B. japonicum* enhanced the salt tolerance by increasing the nutrient uptake (P), root length and proline content (190). Similarly, maize plants colonized with *Rhizophagus intraradices* and *Massilia* sp. (bacteria) displayed enhanced salinity tolerance (191). *Phaseolus vulgaris* cv Valentino plants inoculated with bacteria *Bacillus megaterium* and AMF *Glomus irradicans* exhibited better vegetative growth, chlorophyll content, antioxidant enzyme activity and yield under high salt conditions (192).

All these reports strongly suggest that the different plant microbes (Table 1) play a very important role in mitigating salinity stress in different plants and can be used to reclaim salty soils.

Alleviation of drought stress in plants by micro organisms

Drought affects plants' morphological, anatomical, physiological and biochemical features. Drought stress alters plant transcriptome and metabolome (193). However, rhizosphere microbes, particularly PGPB and PGPF, can help plants cope with water constraints by altering their structural and functional components (194, 195). "Induced systemic tolerance" (IST) is a term that has been used to describe physical and chemical changes brought about by PGPB that make the plant more resistant to abiotic stimuli (196). Inherent metabolic and genetic capabilities of mi-

Table 1. List of the rhizosphere-isolated microorganisms that confer salt stress resistance.

Microorganisms	Plant rhizosphere used for PGPR extraction	Host plant	Responses of plant subjected to salt stress	Reference
Bacillus mojavensis S1 and *Pseudomonas fluorescens* S3	*Hordeum maritimum*	*Hordeum vulgare* cultivar cv. Rihane	Improved root development and enhanced water and nutrient phytoptake	(145)
Aneurinibacillus aneurinilyticus and *Paenibacillus* sp.	*Allium sativum*	*Phaseolus vulgaris*	Increased chlorophyll levels, length, fresh weight and biomass of root and shoot	(151)
Leclercia adecarboxylata MO1	*Solanum lycopersicum*	*Solanum lycopersicum*	Conferred salinity tolerance by modulating levels of sugar, amino acids, organic acids and ABA	(152)
Bacillus aryabhattai PM34	*Solanum tuberosum*	*Triticum aestivum*	Increased germination percentage and length as well as biomass of root and shoot	(153)
Bacillus marisflavi CHR JH 203 and *Bacillus cereus* BST YS1_42	Soil of leguminous crops	*Pisum sativum*	Increased biomass, chlorophyll, flavonoids, sugars and antioxidant enzyme levels	(154)
Rhizobium and *Azotobacter*	*Cicer arietinum*	*Cicer arietinum*	Enhanced nitrogen levels in shoot and root and dry weight, the protein content of seeds and nodule number	(157)

Halomonas sp. and *Bacillus* sp.	*Salicornia rubra*, *Sarcocornia utahensis* and *Allenrolfea occidentalis*	*Medicago sativa*	Enhanced plant growth	(166)
Pseudomonas PS01	*Zea mays*	*Arabidopsis thaliana*	Increased rate of seed germination and survival	(167)
Bacillus tequilensis and *Bacillus aryabhattai*	*Oryza sativa*	*Oryza sativa*	Enhanced photosynthesis, stomatal conductance, transpiration and yield.	(168)

crobes make them suitable opponents for environments with extreme conditions. Some spore-producing microbes produce drought-resistant spores which may last for a very long period in dormant forms. Certain microorganisms can withstand drought because of the thick peptidoglycan in their cell walls. Some microbes may develop a range of tolerance mechanisms, including the regulation of resistance genes, alteration of the metabolism of carbon and nitrogen, production of amino acids, osmolytes, non-reducing sugars and other techniques that counterbalance water loss and safeguard the microbial cell from drought (195). Plant growth promoting bacteria are the members of different bacterial families like *Bacillus, Rhizobium, Burkholderia, Pseudomonas, Azospirillum, Klebsiella, Paenibacillus, Azospirillum, Azotobacter* and *Serratia* etc. and resistance to water stress in plants is mainly determined by the variation in these PGPB (196). *Enterobacter hormaechei*, *Pseudomonas migulae* and *P. fluorescens* (by making exopolysaccharide; EPS) improved foxtail millet (*Setaria italica*) drought tolerance (197). *Vigna mungo* (black gram) and *P. sativum* plants under drought stress were inoculated with rhizobacteria such as *Ochrobactrum pseudogrignonense*, *B. subtilis* and *Pseudomonas* sp. that produce the enzyme ACC deaminase, resulted in enhanced production of ROS-scavenging enzymes and cellular osmolytes, root length, leaf chlorophyll and relative water content (RWC) and controlled ET levels (198).

Drought-associated plant hormones such as IAA, JA, SA and ABA can alter the microbial community structure and their activity (respiration rates) in soil under drought stress (199). Plants under drought stress have higher SA levels. SA helps to reduce the effects of drought damage by strengthening the antioxidant system, raising relative water and proline contents and controlling other phytohormones production. Salicylic acid treatments successfully reduced the negative effects of drought by increasing the activity of antioxidant enzymes, photosynthetic performance and membrane permeability. In wheat under drought stress, SA application at 100 mM increased the activities of antioxidant enzymes, membrane stability, chlorophyll content and photosynthetic rates (200). Endogenous SA is an essential hormone intermediate in *B. subtilis* defense responses that also paved the way for the development of 2 different drought tolerant wheat genotypes (201). Through several mechanisms, including the production of polysaccharides (that improve the soil's ability to retain water and its structure) and the synthesis of deaminase, IAA and proline, soil microorganisms can make plants more resistant to drought (202).

In drought-exposed soils, the relative abundance of saprophytic fungal and arbuscular mycorrhizal indicator species enhanced in response to phytohormones (203). To resist drought stress, AMF was shown to improve water absorption, nutrient uptake, root structure, photosynthetic activity, antioxidant activity, fatty acid and polyamine homeostasis, osmotic balance, aquaporin expression, hormone balance and soil structure by releasing glomalin which regulates plant-soil water relations (204-206). Numerous biotic and abiotic elicitors, such as ketoconazole, alginate-derived oligosaccharides, 2-aminoethanol, brassinosteroids, ABA and advantageous microorganisms like *Rhizobium* strains, AMF, can increase the plant's ability to tolerate drought stress (193). Upon inoculating Trifoliate orange (*Poncirus trifoliata*) leaves with *Paraglomus occultum* and *Funneliformis mosseae*, a change in the activity of proline and sucrose-metabolizing enzymes was detected (207). As a strategy to promote sustainable water consumption during drought, the AMF inoculation affected the physiological responses and leaf proline content in *Glycine max* (208). In chickpea (*C. arietinum* L.), inoculation of AMF (*Rhizophagus irregularis, Claroideoglomus etunicatum* and *F. mosseae*) and biochar improved drought tolerance by increasing nitrogen fixation, number and mass of nodules, leghemoglobin content and nitrate reductase activity (209). Silicon (Si) and *Rhizophagus clarus* (AMF) mitigated drought stress by dramatically improving plant biomass production by enhancing photosynthesis, increasing the water content and usage efficiency, an antioxidant enzyme and nutritional quality mainly Zn in strawberries (210). Arbuscular mycorrhizal fungal colonization protected the photosynthetic apparatus by alleviating drought-induced damage to PSII and PSI structure and function in *T. aestivum* (wheat) (211).

When inoculated with AMF, *Leymus chinensis* (C3 plant) and *Hemarthria altissima* (C4 plant) plants displayed increased growth and photosynthesis (212). In maize, AMF alleviated drought-induced impacts on growth and physio-biochemical characteristics by dramatically enhancing chlorophyll content, mineral absorption and assimilation. Arbuscular mycorrhizal fungi mediated up-regulation of the antioxidant system, maintained redox equilibrium, protected critical metabolic pathways, including photosynthesis and increased proline levels, sugars and amino acids (26). In response to drought stress, AMF, *F. mosseae*, boosted the activity of H^+-ATPase in *P. trifoliata's* root and leaf and *PtAHA2* gene expression, resulting in improved nutrient absorption, root development and a low soil pH microenvironment (213).

Recently it was reported that drought-exposed *Sesamum indicum* plants treated with *F. mosseae* and *R. intraradices* resulted in increased mycorrhizal root colonization, soluble protein, seed and oil yield, chlorophyll, P, unsaturated fatty acids and non-enzymatic antioxidants. They also observed a decrease in saturated fats and the proportion of saturated to unsaturated fats (214). The interaction of both AMF (*G. mosseae*, *Glomus etunicatum*) and PGPB (*Azotobacter chroococcum*, *Azospirillium lipofrum*) increased growth in *Juglans regia* (walnut) under the drought stress by significantly increasing proline, starch content, phenol content, total soluble sugar and POD activity (215). PGPR helps in reducing the effects of drought stress by forming colonies in the root-zones and promoting plant growth under various conditions. They can also solubilize different micronutrients to make them absorbable by plants. Rice plants inoculated with phyllosphere bacteria (isolated from phyllosphere of Anna R(4), Mattaikar, PMK3 and Nootripattu rice varieties) displayed drought stress resistance (216). Five ACC deaminase-producing bacteria namely *Pseudomonas stutzeri, Acinetobacter* sp*., B. mojavensis, Pseudomonas chlororaphis* and *Enterobacter asburiae* isolated from cotton's phyllosphere were found to improve plant growth during drought conditions through the siderophores and IAA production and also solubilization of phosphate, zinc and potassium (217). Effect of plant growth-promoting organisms mix containing beneficial species of mycorrhiza, *Trichoderma*, bacteria and yeasts were studied on photosynthetic activity, leaf anatomy and plant growth of soybean cv. "Pr91m10". It was reported that the leaves of inoculated plants had a higher density of smaller stomata, thicker palisade parenchyma and larger intercellular spaces in the mesophyll. Leaf anatomical changes also impact gaseous exchange and during the reproductive phase inoculated plants exhibited higher photosynthetic rate as compared to control plants (218).

Some of the microorganisms that significantly confer drought stress tolerance to various plants are listed in Table 2.

Amelioration of temperature stress in plants by microorganisms

Temperature stress represents an important abiotic stress observed in plants. It is caused by temperature extremes, i.e. heat and cold stress. The prevalence of very high temperatures adversely affects plants as it leads to wilting of leaves, retarded growth, abscission and senescence of leaves, protein denaturation, aggregation, reduced permeability of membranes, increased oxidative stress, reduced yield etc. (232). Similarly, the presence of extremely low temperatures is highly undesirable for plants as it leads to various physiological changes in plants like chlorosis, necrosis, crystallization of cellular water, increased relative

Table 2. Microorganisms responsible for conferring drought stress tolerance.

Microbes	Host Plant	Effect	Reference
AMF species			
Glomus versiforme	*Citrullus lanatus*	Higher antioxidant enzymes activities, higher non-photochemical quenching values, increased soluble sugar and proline contents	(219)
Glomus fasciculatum, G. mosseae, Gigaspora decipiens	*Triticum aestivum*	Enhanced plant developmental characteristics and total chlorophyll pigments	(220)
Paraglomus occultum *F. mosseae*	*Poncirus trifoliata*	Increased length of hyphae, rate of water absorption and water potential	(221)
F. mosseae	*Zea mays*	Efficient root hydraulic	(222)
F. mosseae	*Poncirus trifoliata*	Changes in polyamines concentration	(223)
Endophytic fungi			
Epichloë festucae	*Lolium perenne*	Enhanced photosynthesis, growth and uptake of P	(224)
Cladosporium oxysporum, *Embellisia chlamydospore*, and *Paraphoma* sp.	*Glycyrrhiza uralensis* and *Zea mays*	Increased root:shoot ratio and biomass	(225)
Trichoderma atroviride	*Zea mays*	ROS scavenging enzymes (SOD, CAT, APX and GR) activity increased and H_2O_2 levels decreased	(226)
Ampelomyces sp.	*Solanum lycopersicum*	Increased growth and yield	(227)
Bacterial species			
Rhizobacteria	*Solanum tuberosum*	Altered ROS-scavenging enzyme expression and increased photosynthesis	(228)
Bacillus thuringiensis	*Lavandula*	Improved physiology, metabolic and nutritional plant properties.	(229)
Bacillus subtilis (LDR2)	*Triticum aestivum*	Increased photosynthetic efficiency	(230)
Azospirillum sp.	*Zea mays*	Accumulation of osmoprotectants and improved growth characteristics	(231)

electrolyte leakage, lower membrane conductivity, reduced relative water content, retarded growth in plants which under extreme conditions may lead to death (233). Several studies have shown that temperature changes due to seasonal variation impacts the microbial composition of the phyllosphere (234). Increased temperature has been reported to have several effects on the diversity and phylogenetic composition of the phyllosphere bacterial community. It was observed that long-term warming increased the bacterial richness and diversity in the phyllosphere (235).

Plant microbiome is crucial in the management of abiotic stress. Microorganisms have been reported to play an important role in temperature stress also owing to the inherent property of thermotolerance. There have been several reports of bacteria, fungi and AMF being used successfully for mitigating high and low-temperature stress. It has been reported that in *Sorghum* seedlings, *Pseudomonas* sp. strain NBRI0987 imparted thermotolerance, due to the synthesis of high molecular weight proteins in the leaves which resulted in improved plant biomass (236).

Bacillus amyloliquefaciens inoculation in wheat was reported to impart tolerance to heat stress by activation of heat shock protein (HSP) TFs and lower production of ROS (237). Chinese cabbage (*Brassica campestris* subspecies *pekinensis*) after inoculation with *B. aryabhattai* H26-2 and *Bacillus siamensis* H30-3 resulted in tolerance to heat and drought stresses by increasing ABA content leading to reduced leaf wilting and reduced stomatal opening (238). The thermotolerant bacterium *B. cereus SA1* inoculation in soybean plants imparted high-temperature stress tolerance by increasing the biomass, chlorophyll content, antioxidant enzyme activity, expression of HSPs etc. (239). Additionally, overexpression of stress-responsive genes *GmLAX3* and *GmAKT2* in inoculated soybean plants could be connected to a decline in the generation of ROS.

A fungus, *Paraphaeosphaeria quadriseptata*, found in the rhizosphere was shown to impart high-temperature stress tolerance to *A. thaliana* by HSP101 and HSP70 expression (240). Inoculation of *japonica* rice plants with *Paecilomyces formosus LWL1* resulted in tolerance to high temperature which was evident by increased chlorophyll content, improved plant height, increased protein content as well as higher dry weight and fresh weight (241).

Similarly, several AMF species have been shown to improve the thermotolerance to heat and cold stress in plants. *Glomus mosseae* showed increased tolerance to both heat and cold stress in *Poncirus trifoliata* through higher biomass of shoot and root biomass (242). Inoculation with AMF cultures of *F. geosporum, F. mosseae* and *R. intraradices* resulted in the ability to impart tolerance to heat stress in *Zea mays* plants. Plants inoculated with AMF showed improved growth, larger root system, the quantum efficiency of PS II, higher chlorophyll content, improved stomatal conductance, higher transpiration rates and photosynthetic rate (243). Inoculation of *T. aestivum* plants with AMF cultures comprising *F. geosporum*, *R. irregularis* and *F. mosseae,* resulted in better allocation of nutrients, higher nutrient composition in roots and improved grain number (244). In a study involving inoculation of *Cucumis sativus* L. cv. Zhongnong No. 26 with AMF *R. irregularis* resulted in higher P content, increased root biomass and up-regulation of the Pi transporter gene of the *Pht1* gene family under cold stress (245). *Solanum melongena* L. plants upon inoculation with cultures of *Diversispora versiformis, C. etunicatum, F. mosseae* and *R. irregularis* imparted tolerance to low-temperature stress by increasing photochemical reactions, reducing membrane damages, improving antioxidant defense system and accumulating protecting molecules (246). A recent report based on meta-analysis covering 39 studies on microbe-mediated tolerance to high-temperature stress and the related mechanisms revealed significant changes in the levels of MDA, H_2O_2, proline, antioxidant enzyme activities, ROS levels, photosynthetic efficiency involving PS II guiding the response among other mechanisms (247).

All these studies, therefore, suggest that plant microbiome (Table 3) plays a crucial role in alleviating temperature stress in plants.

Microorganisms and heavy metal stress tolerance

HM contamination is regarded as a significant source of pollution in the environment. Heavy metals do not undergo chemical degradation and stay in the soil for a very long period thereby causing harm to the soil and the environment. Heavy metals pose several detrimental impact on plant growth and development. Various HM-resistant endophytes promote plant growth via various mechanisms, which include nitrogen fixation, mineral solubilization and phytohormones and siderophores production.

PGPR appreciably improves root development and plant growth by enhancing plant tolerance against metal stress (259). Consequently, healthy plants with strong roots and shoots can eliminate both organic and inorganic impurities. PGPB genera including *Bacillus, Beijerinkia,*

Table 3. Microorganisms responsible for conferring temperature stress tolerance.

AMF species	Host Plant	Stress	Effect	Reference
Glomus etunicatum	*Zea mays*	Low temperature	Improved water conservation and water use efficiency, increased osmotic adjustments, increased efficiency of PS II	(248)
Glomus mosseae	*Lycopersicon esculentum* cv. Zhongzha105	Low temperature	Decreased membrane lipid peroxidation, increased photosynthetic pigments, improved antioxidant enzymes activity	(249)
Funneliformis mosseae	*Cucumis sativa*	Low temperature	Increased fresh and dry weight, improved secondary metabolite content, increased expression of stress-related marker genes	(250)
Glomus fasciculatum	*Cyclamen*	High temperature	Increased biomass production, increased antioxidant enzymes activities, increased ascorbic acid and polyphenol contents	(251)

Bacterial species				
Pseudomonas putida strain AKMP7	*Triticum aestivum*	High temperature	Increased dry weight, root length, tillers, shoot length, higher levels of several metabolites, increased grain and spikelet formation	(252)
Bacillus amyloliquefaciens, Azospirillum brasilense	*Triticum aestivum*	High temperature	Reduced production of ROS, activation of HSP TFs	(237)
Paraburkholderia phytofirmans strain PsJN	*Lycopersicon esculentum* L.	High temperature	Increased chlorophyll content, proline content, and total amino acids along with enhanced PS II activity.	(253)
B. cereus, Providencia rettgeri, Myroides odoratimimus	*Sorghum bicolor*	High temperature	Increased plant growth, increased antioxidant enzyme activities, decreased proline and MDA content	(254)
Fungal species				
Endophytic Ascomycetous mitosporic fungi strain SMCD 2210, 2215 , 2206, 2204, 2208 and 2215	*Triticum aestivum*	High temperature	Increased plant height, increased seed weight, enhanced germination rates, improved efficiency of PS II	(255)
Chaetomium sp.	*Oryza sativa*	High temperature	Improved shoot growth, improved root growth, increased survival percentage	(256)
Aspergillus violaceofuscus	*Helianthus annuus*; *Glycine max*	High temperature	Increased chlorophyll content, decreased levels of ROS, proline, ascorbic acid *etc.*	(257)
Aspergillus aculeatus	*Lolium perenne*	High temperature	Enhanced efficiency of photosynthetic apparatus, reduced activities of antioxidant enzyme	(258)

Burkholderia, Erwinia, Enterobacter, Flavobacterium, Gluconacetobacter, *Klebsiella, Pseudomonas, Serratia* have been shown to enhance plant growth (14). Plant growth-promoting rhizobacteria like *Pseudomonas brassicacearum* and *Variovorax paradoxus* with ACC deaminase activity reduced the toxic effect of HMs and mitigated the negative impact of ET on *P. sativum* and *Brassica juncea* plants under various environmental circumstances (260). *Alcaligenes feacalis* KP717561, *B. subtilis* KP717559 and *Pseudomonas aeruginosa* KP717554 facilitated the accumulation of HMs namely Cr, Cd and Ni in roots and shoots of *Brassica juncea*. Additionally, Ni uptake in the shoots of *B. juncea* increased due to the solubilization of P and synthesis of IAA that promoted the plant root and shoot growth (261). Several arsenic-resistant bacteria like *Bacillus indicus, Bacillus arsenicus* (262), *Shewanell* sp. (263), *Enterobacter* (264), *Ochrobactrum intermedium* (265) and *Providencia alcalifaciens* (266) have also been reported to confer HM tolerance.

Sorghum bicolor plants when injected with *Streptomyces mirabilis* “P16B-1” showed metal stress tolerance (267). Inoculation with *Streptomyces* sp. HM1 in maize plants increased the chlorophyll content and provided resistance against Cd (268). Similarly, *Rhodococcus erythropolis* in polluted soil reduced Cr absorption and increased *P. sativum* plant growth mainly through IAA synthesis and P solubilization (267). Several rhizospheric bacteria also synthesize siderophores which chelate Fe^{3+} and different forms of iron are then absorbed by the plants (269). *Streptomyces cyaneus* and *Streptomyces rapamycinicus* restored the Cd absorption and accumulation within *Chlorophytum comosum* plants (270). It was further reported the use of *Streptomyces phaeogriseichromatogenes* for Cd phytoremediation and sunflower growth promotion potentials (271). Heavy metal resistant siderophore-producing bacteria (SPB), *Burkholderia* sp. strain SX9 have been shown to improve the germination of *Lolium perenne* seeds subjected to HM stress (272). *Pseudomonas* sp. TR15a is produced by the consortium of ACC enzymes and the production of siderophore by *Bacillus aerophilus*. TR15c played a crucial part by enhancing Cu uptake and increasing biomass and thus can be used as a different approach for the decontamination of Cu-polluted ecosystems (273). Further, Ni-resistant endophytic bacteria (NiEB), *Stenotrophomonas* sp. S20, *Sphingobium* sp. S42 and *Pseudomonas* sp. P21 isolated from wetland *Tamarix* plants can tolerate desert heat and also synthesize plant growth-promoting substances namely, IAA, siderophores and ACC enzymes and can remediate HM contaminated soils (274).

Many mycorrhizal fungi have been shown to hyperaccumulate metals in metal-polluted soil and have been shown to play a role in phytoremediation (275). Arbuscular mycorrhizal fungi and earthworms inoculated *Solanum nigrum* plants displayed improved growth and increased productivity in Cd-polluted soil (276). *Gluconacetobacter diazotrophicus* and *P. aeruginosa* (CMG 823) produce derivatives of gluconic, 5-ketogluconic acid involved in solubilizing Zn compounds and can thus be used as biofertilizers which help in enhancing soil quality and plant development (277). A fungal endophyte namely *Trametes hirsuta* isolated from *Chenopodium album* growing in Pb-polluted soil helped in the phytoextraction of HMs from polluted sites and conferred lead tolerance to *T. aestivum* L. seedlings (278). Symbiotic nitrogen-fixing rhizobacterial genera like *Bradyrhizobium*, *Mesorhizobium, Rhizobium* etc. enhanced the growth and development of legumes in metal-contaminated soils (279).

The immobilization of Cd in the rhizosphere by PGPR and plant nutritional fertilizers based on nanohybrids would be a sustainable prospective method to immobilize phytoavailable Cd and detoxify plant cells (280). Plants of *Lathyrus sativus* inoculated with *P. fluorescens*

(K23), *Rhizobium leguminosarum* (M5), *Variovorax* sp. and *Luteibacter* sp., decreased the lead and Cd available in the "rhizospheric soils" by accumulating them in shoots and roots (281). Silicon within the spores and hyphae of AMF has also been recognized as an environment-friendly approach that enhances stress tolerance by reducing toxic ion uptake, nutrient uptake, upregulation of plant metabolic processes and increased root rhizosphere. Thus, AMF and Si possess relative roles in mitigating salinity and HM stresses and their dual functions aid in the stress control of crop plants (282). Some of the microorganisms that contribute to HM stress tolerance are provided in table 4.

Plants and Pesticide stress

Pesticides are chemicals used to control rats, fungi, insects and other pests. Pesticides have the potential to pollute grassland, water and other vegetation. Pesticides can be poisonous to a variety of different organisms in addition to insects and weeds, such as birds, fish, helpful insects and non-target plants (312-314). Since pesticides have the potential to enter into the environment either directly or through the plants, it is very essential to remediate the same as some of the transformed products of the pesticides might be further harmful to plants and animals. Pesticides have the ability to negatively affect agricultural physiology, particularly on photosynthesis, which could reduce crop growth and output (315). The application of pesticides to plants leads to toxicity, which manifests itself in the form of necrosis, chlorosis, stunting, burns and twisting of the leaves (316). In *Nostoc*, the application of

Table 4. Microorganisms responsible for conferring heavy metal stress tolerance.

Plant	Microorganism	Metal Stress	Effect	Reference
Vigna unguiculata	*Photobacterium* species strain MELD1	Hg	Enhanced growth in Hg-polluted soil; increased Hg absorption in roots; considerably lower levels of Hg in pods	(283)
Brassica oxyrrhina	*Pseudomonas libanensis* TR1, *Pseudomonas reactans* Ph3R3	Cu, Zn	Enhanced plant growth, leaf pigment, and relative water content and decline in MDA and proline levels in leaves	(284)
Vitis vinifera	*Micrococcus luteus*	As (Arsenic)	Increased plant biomass and protein content and enhanced CAT and POD activity in presence of high $NaAsO_2$ concentration	(285)
Trifolium arvense	*Pseudomonas azotoformans*	Cu, Zn, Ni	Enhanced phytoremediation efficiency of *Trifolium arvense* plants grown in soil contaminated by HMs under drought stress	(286)
Brassica juncea	*Streptomyces pactum*	Zn, Pb, Cd, Cu	Increased absorption of Zn (40, 14%) and Pb (82, 15%) in roots and shoot and Cu and Cd in root	(287)
Centella asiatica L	*Enterobacter* sp. *FM-1*	Cd	Enhanced Cd contents in stems, leaves and roots of plants	(288)
Brassica rapa, Brassica campestris	*Bacillus megaterium* H3	Cd	Enhanced soluble proteins, edible tissue biomass and, vitamin C content and reduced Pb and Cd absorption by the edible tissues	(289)
Raphanus sativus	*Serratia liquefaciens* and *Bacillus thuringiensis*	Cd and Pb	Reduced soil Cd and Pb availability and increased Cd or Pb movement from the roots to the leaves to reduce Cd and Pb absorption by edible tissue	(290)
Vigna mungo	*Klebsiella pneumonia*	Cd	Proline and antioxidant enzymes such as POD and APX, in greater amounts as well as improved plant development increased germination percentage, root and shoot length and biomass	(291)
Helianthus annuus	*Trichoderma* sp.	As, Pb	Increased As and Pb accumulations in shoots	(292)
Pennisetum purpureum	*Micrococcus* sp.	Cd	The roots and shoots displayed enhanced Cd accumulation.	(293)
Cicer arietinum	*Pseudomonas* sp.	Ni	Enhanced biomass and decreased metal absorption	(294)
Lycopersicon esculentum	*Pseudomonas aeruginosa* and *Burkholderia gladioli*	Cd	Increased fresh weight, shoot length, root length and photosynthetic efficiency	(295)
Miscanthus sinensis	*Chaetomium cupreum*	Al	Production of siderophores, increased Al tolerance via production of oosporein and chlorogenic acid	(296)
Phragmites communis	*Simplicillium chinense*	Cd and Pb	Pb and Cd biosorption	(297)
Brassica juncea	*Bacillusmucilaginosus* HKK-1	Zn	Increased bioavailability of metals and biomass	(298)
Helianthus annuus	*Pseudomonas libanensis* TR1, *Claroideoglomus claroideum* BEG210	Ni	Enhanced Ni and Na accumulation under salinity and Ni stress alone or in combination	(299)
Sedum plumbizincicola	*Rhodococcus* sp. NSX2	Cd	Increased Cd accumulation phytoremediation efficiency	(300)
Sesbania rostrata	Rhizobia and AMF	U	Increased plant biomass and uranium accumulation	(301)
Brassica juncea	*Serratia* PRE01, *Arthrobacter* PRE05	V	Enhanced absorption of metals and biomass	(302)
Cajanus cajan	*Proteus vulgaris* KNP3	Cu	Increased biomass, germination and chlorophyll content	(303)

Ricinus communis	*Pseudomonas* sp. M6	Ni	Enhanced biomass and production of IAA	(303)
Eichhornia crassipes	*Pseudomonas diminuta*	Cr	Increased metal absorption	(303)
Sedum alfredii	*Pseudomonas fluorescens*	Cd	Promotion of lateral root development in host plants, which enhanced the efficiency of Cd phytoremediation	(304)
Zea mays	*Serratia* sp.	Zn	Enhanced growth, antioxidant enzymes activities and decreased Zn accumulation when exposed to Zn stress	(305)
Oryza sativa	*Piriformospora indica*	Cd	Endure Cd toxicity by relieving oxidative stress	(306)
Triticum aestivum	*Enterobacter bugandensis* TJ6	Cd and Pb	Secretion of IAA, arginine, and betaine under Cd and Pb stress; phytohormones levels, DNA repair and plant antioxidant activity increased when under stress	(307)
Triticum aestivum	*Bacillus megaterium N3*	Cd	Decreased Cd content in wheat roots and improved expression of proteins involved in DNA repair	(308)
Combretum erythrophyllum	*Methylobacterium radiotolerans*	Zn, Cu, and Ni	Zn, Cu and Ni-resistant proteins present in the bacteria confer heavy metal resistance to plant	(309)
Triticum aestivum	*Bacillus halotolerant* J143, *Enterobacter hormaechei* J146 and *Pseudomonas frederiksbergensis* J158	Zn	Improved seed germination, plant growth in wheat and Zn absorption	(310)
Alfalfa	*Bacillus subtilis*	Cd	Improved growth and Cd uptake ability; regulation of metabolite levels of amino acids, fatty acids, carbohydrates and flavonoids	(311)

endosulfan resulted in the deactivation of photosystem II along with the suppression of the activity of nitrogenase (317). In *P. vulgaris*, treatment with chlorpyrifos resulted a decrease in the length of the stem and leaf as well as a reduction in the number of pods. In addition, there was a reduction in photosynthetic pigments and lipids in the leaf and a lowering of the levels of triglycerides in the fruits (318). In *Chlorella vulgaris*, quinalphos and chlorfenvinphos reduced OJIP fluorescence at all levels by reducing the percentage of PS II reaction centers that reduce Q (A). Dimethoate and phorate decreased OJIP fluorescence by impeding the movement of electrons beyond Q(A). By increasing the dissipated energy flux per active reaction center, insecticide treatment led to a decrease in the density of active reaction centers and performance indices (PI). Treatment with quinalphos and chlorfenvinphos drastically reduced antenna size (319).

The most prominent and fundamental response of pesticide stress in plants is oxidative stress and activation of the antioxidant defense system (320, 321). Pesticides raise the amounts of superoxide (O_2•-) and NADPH oxidases (NOXs), which increases ROS signaling in the cell. High ROS may cause the oxidation of lipids, proteins and DNA which can result in a number of toxicities (322). The effect of pesticides on redox homeostasis has been extensively studied in different systems. Plants that are regularly exposed to pesticides for an extended period experienced a notable alteration in antioxidant enzyme levels. In a study on *Allium cepa*, it was found that the application of malathion resulted in the downregulation of APX and GR. On the other hand, the activities of SOD, CAT and glutathione S transferase were increased. This was also accompanied by an increase in the magnitude of lipid peroxidation (323). In another study, it was observed that the application of organophosphate compounds namely malathion and tatafen altered the mRNA expression of APX, CAT and Fe-SOD in *Solanum melongela* Cv *Longai* (324). In another experiment, the application of 1-[6-chloro-3-methyl-pyridyl-8-nitro-7-methyl-1 2 3 5 6 7-hexahydro imidazo (1,2a)]-pyridine in wheat altered the functioning of SOD, guaiacol peroxidase, CAT and polyphenol oxidase. This was accompanied by an increase in the activities of MDA (325). In a recent study, it was observed that tomato plants treated with diazinon, imidacloprid and mancozeb increased the generation of ROS. This was accompanied by an alteration in mitochondrial membrane potential. In addition, a significant increase in the level of antioxidant enzymes namely APX, CAT, SOD, POD and guaiacol peroxidase (321). In another similar study, application of emamectin benzoate, alpha-cypermethrin and imidacloprid in tomatoes resulted in an increased concentration of ROS along with the formation of thiobarbituric acid reactive substances resulting from membrane damage. In addition, there was an increase in the activities of the antioxidant enzymes (326).

Engineering abiotic stress tolerance in plants by transforming microorganisms' genes

In comparison to traditional breeding, genetic engineering has the advantage of being able to modify plants with desirable traits for phytoremediation in a lot less time. Genetic engineering has been proven to be a promising technique for improving the phytoremediation abilities of plants toward HM pollution. Furthermore, desirable genes from microbes can even be transferred via genetic engineering to species of sexually incompatible plants, which is not conceivable using conventional breeding techniques like crossing. Consequently, the use of genetic engineering to create transgenic plants with the necessary features has offered a promising future for phytoremediation (327). Plants can be genetically modified to overexpress certain genes involved in the metabolism, absorption or transport of particular contaminants, directly boosting the efficacy of phytoremediation. Using *Agrobacterium tumefaciens*-mediated plant transformation, the introduction of these genes can be easily accomplished for many plant species

(328). As discussed in previous sections, the microbes are equipped with tremendous potential to remediate contaminants from the atmosphere. They have a unique genetic machinery that enables them to degrade or extract contaminants. This unique genetic machinery or more precisely the genes responsible for the same are being targeted by scientists to develop transgenic plants. Suplemantary table describes selected genes that have been engineered in plants with positive outcomes and showed the potential of bioremediation.

Future perspectives

Agricultural productivity is significantly affected by fluctuating environmental conditions. Future research demands delineation of the mechanism of interaction, growth enhancement and signaling during different abiotic stress conditions. Identification of genes and novel microbes conferring abiotic stress tolerance to plants will further aid in developing high-yielding stress-resistant plants. Plant growth promoting microorganisms should also be pushed as a biofertilizer for plant development and commercialized for sustainable agriculture productivity since they are a great replacement for chemical fertilizers owing to their low cost and eco-friendly nature. Field experiments must be performed and farmers must be made aware of the advantages of soil microorganisms. Entrepreneurs should invest in biofertilizer businesses more frequently and give funding to start-ups. Given the facts above, it is clear that we are headed in the correct direction in terms of accomplishing our objective of sustainable agricultural production in a climate that is constantly changing.

Conclusion

Mitigation of different abiotic stresses by the plant microbiome has been examined in depth in this review. Different studies suggested that microorganisms can alleviate abiotic stresses in plants. These studies will offer new directions for increasing the productivity of plants in changing climatic conditions. Although it is a lengthy procedure, it is possible to generate stress-tolerant plants through genetic engineering. The use of microbes for conferring stress tolerance is a less time-consuming, cheaper and environment -friendly method. To resolve food security issues worldwide, future work demands the characterization of a wider array of potential stress-resistant microorganisms and the different mitigation mechanisms they practice to alleviate abiotic stress.

Authors contributions

RM conceived and designed the outline of the review. RS, GP, SS, DS and RM collected the data and wrote the paper. All authors have read and approved the final manuscript. All authors gave equal intellectual inputs in composition of the manuscript.

Compliance with ethical standards

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Supplementary data

Supplementary Table . Selected genes engineered in plants to develop transgenics that could be utilized for remediation of environmental contaminants.

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