



Plant-Microbe Interactions in Alleviating Abiotic Stress—A Mini Review

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Crop plants are continuously exposed to various abiotic stresses like drought, salinity, ultraviolet radiation, low and high temperatures, flooding, metal toxicities, nutrient deficiencies which act as limiting factors that hampers plant growth and low agricultural productivity. Climate change and intensive agricultural practices has further aggravated the impact of abiotic stresses leading to a substantial crop loss worldwide. Crop plants have to get acclimatized to various environmental abiotic stress factors. Though genetic engineering is applied to improve plants tolerance to abiotic stresses, these are long-term strategies, and many countries have not accepted them worldwide. Therefore, use of microbes can be an economical and ecofriendly tool to avoid the shortcomings of other strategies. The microbial community in close proximity to the plant roots is so diverse in nature and can play an important role in mitigating the abiotic stresses. Plant-associated microorganisms, such as endophytes, arbuscular mycorrhizal fungi (AMF), and plant growth-promoting rhizobacteria (PGPR), are well-documented for their role in promoting crop productivity and providing stress tolerance. This mini review highlights and discusses the current knowledge on the role of various microbes and its tolerance mechanisms which helps the crop plants to mitigate and tolerate varied abiotic stresses.

Keywords: abiotic stress, AMF, endophytes, mitigation, nutrient uptake, PGPR, tolerance mechanism

INTRODUCTION

Agriculture is one among the most important essential sectors which is of utmost susceptible to global climate changes. The rapid increase in population with unplanned industrialization, intensive agriculture has led to the degradation of natural resources and environmental contamination (Wan et al., 2012). The increase in the incidences of abiotic stresses affecting crop productivity are being witnessed throughout the world. Crop plants are often exposed to various environmental stresses such as drought, soil acidity, salinity, ultraviolet radiation, high light and extreme temperatures, deficiencies and toxicities of mineral nutrients which severely affects the soil productivity and crop production, worldwide. Based on the report by Food and Agriculture Organization (FAO, 2016), the agricultural production has to be increased by about 60% by 2050 to feed the increasing global population. Moreover, due to the global climate change accompanied with the other abiotic stresses there will be a decline in the production of major cereal crops (20–45% in maize yields, 5–50% in wheat, and 20–30% in rice) by the year 2100. The adverse impacts on crop productivity are progressing at an exponential rate due to the direct and indirect effects of abiotic stresses. The worldwide drastic climatic changes along with the rapid increase in the global population has become a major threat to Global food security (Lesk et al., 2016). The resilience

of crops to various abiotic stresses has to be augmented to ensure high crop productivity in challenging environments to meet the demands of growing population (Pereira, 2016).

Oxygen is essential for the existence of aerobic life, but toxic reactive oxygen species (ROS), which include the superoxide anion radical ($O_2^{\bullet-}$), hydroxyl radical (OH^{\bullet}), and hydrogen peroxide (H_2O_2), are generated in all aerobic cells during metabolic processes. Injury caused by these ROS is known as oxidative stress, which is one of the major damaging factors to plants exposed to various environmental stresses which causes extensive cellular damage disrupting the photosynthesis and other physiological functions in plants (Mhamdi and Breusegem, 2018). To mitigate the adverse effect of ROS, plants do respond through the release of enzymatic [superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), and peroxidase (POD)] and non-enzymatic antioxidants (glutathione, carotenoids, and ascorbates) as a protective mechanism (Sharma et al., 2012).

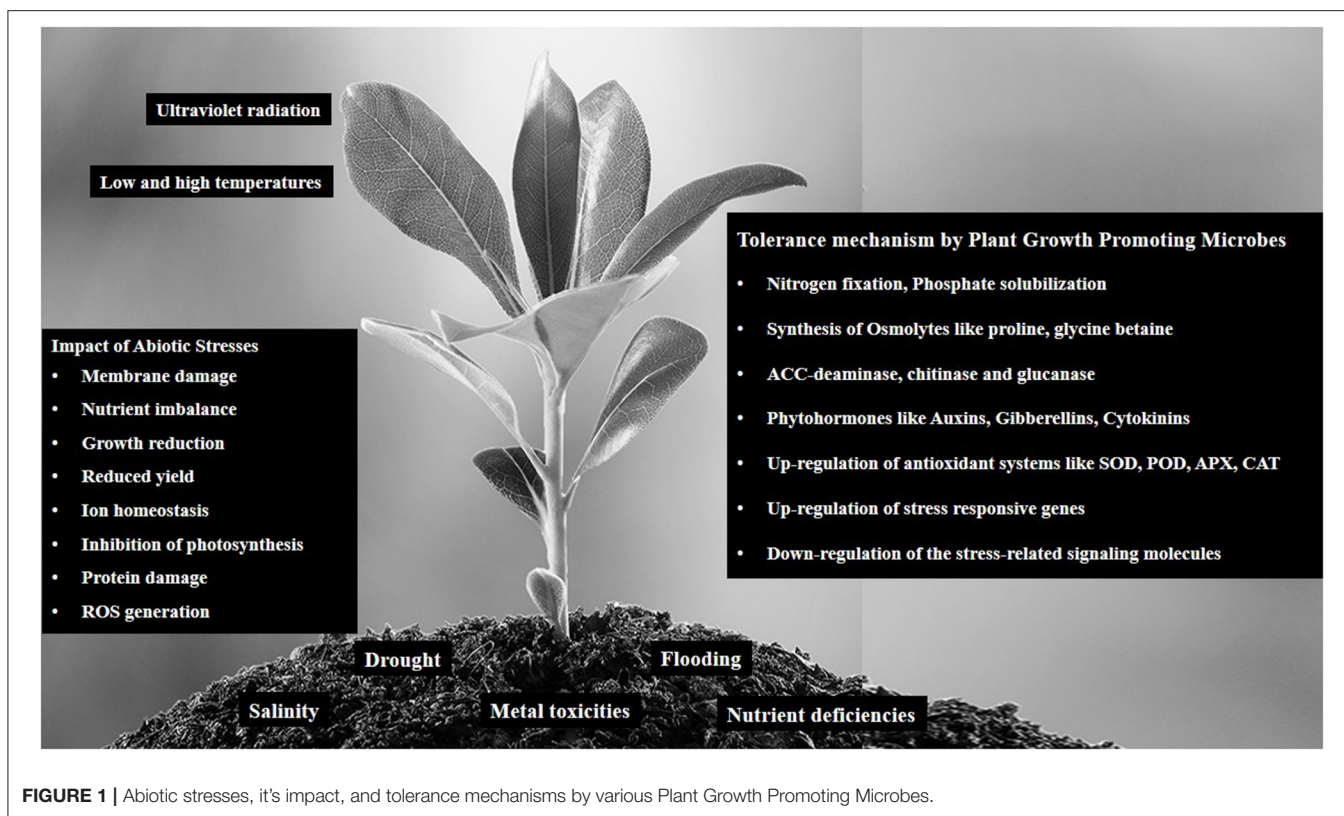
To overcome the adverse effects of abiotic stresses, the application of microbes is an effective, ecofriendly and economically viable method. The nutrition required for the microbial growth is provided by the root exudates which makes the “rhizosphere” microbial population comparatively diverse from that of its surroundings (Burdman et al., 2000). The microbial biome either living inside or in close vicinity to the plants play a vital role in fighting against the various environmental stresses and has substantially impact on plant growth and development (Hayat et al., 2010; Friesen et al., 2011; Bhattacharyya and Jha, 2012; Bulgarelli et al., 2013; Naeem et al., 2018). Thus, the present concise review highlights and discusses the role of microbes as a biological tool for alleviating and enhancing crop growth under environmental stress conditions.

EFFECT OF ABIOTIC STRESSES ON CROPS

Abiotic stresses like salinity, drought, heavy metals, nutrient deficiency, high and low temperatures remain major contributors of agricultural losses, and cause more damage to the crops (Figure 1). Soils contaminated with various heavy metals has become a serious environmental concern because of its adverse impact on the agricultural lands. Heavy metal contamination has deleterious effects on several plant physiological functions which ultimately decreases crop productivity which results in severe quantity and quality losses (Hashem et al., 2016). The excess accumulation of heavy metals in plant tissues can have adverse effects on the plants directly or indirectly right from germination of seeds, photosynthesis to poor crop yield (Uzu et al., 2009). Rapid increase in the number of various industries and the use of saline water for crop cultivation is yet another major problem which affects the crop production. Salinity stress conditions has become a major issue which leads to poor crop productivity and is alarmingly increasing in arable land all over the world (Yuan et al., 2015). High salinity significantly impacts various physiological and biochemical processes in plants, such as seed germination, seedling establishment, vegetative growth, ionic

toxicity, osmotic pressure, and oxidative damage (Zhao et al., 2010; Feng et al., 2014; Guo et al., 2018). Moreover, high salinity is interlinked with drought, yet another major issue, which can be magnified by extreme temperatures (Slama et al., 2015). Drought stress has significant negative impact on the two photosystems; PSI and PSII, in Kentucky bluegrass and fescue (Fu and Huang, 2001) and can be detrimental to enzyme functioning such as ascorbate peroxidase (APX), glutathione reductase (GR), and superoxide dismutase (SOD) (Hoekstra et al., 2001). Tiwari et al. (2016) have reported that two chickpea cultivars grown under drought stress conditions had significant impact on various growth parameters, water status, membrane integrity, osmolyte accumulation, ROS scavenging ability and stress-responsive gene expressions. Cold stress on the other hand, leads to cell and tissue dehydration, cellular water crystallization, reduced membrane conductivity, higher relative electrolyte leakage (REL), decreased weight, lower relative water content (RWC), and ultimately leading to poor crop yield (Browse and Xin, 2001; Pearce, 2001; Jia et al., 2017). *Stevia rebaudiana* Bertoni grown under cold stress conditions led to a significant decrease in the maximum quantum yield of photosystem II (F_v/F_m), reductions in net photosynthesis (P_N), intercellular CO_2 (C_i), water use efficiency (WUE), and chl *a*, chl *b*, and carotenoids (Hajihashemi et al., 2018).

The increase in global average temperature can have an alarming impact on the crop production worldwide and can change the pattern of agricultural crops distribution (Porter, 2005). High temperature stress can cause severe protein damage, protein synthesis, enzyme inactivation, membrane damage, root growth, uptake of water and nutrients, oxidative damage, and decreased photosynthetic rate (Smertenko et al., 1997; Wahid et al., 2007; Huang et al., 2012; Djanaguiraman et al., 2018). The photosystem II (PSII) is extremely sensitive to high temperature stress wherein it severely damages the oxygen-evolving complex (OEC) and denaturation of D1 and D2 proteins (De Las Rivas and Barber, 1997; De Ronde et al., 2004; Camejo et al., 2005). Soybean plants grown in open top chambers which were exposed to elevated ozone or/and UV radiations significantly decreased the seed which was directly associated with changes in the concentrations of flavonoids, abscisic acid (ABA) and indole-3-acetic acid (IAA) (Mao et al., 2017). Sugar beet plants under UV-B induced stress conditions showed reduced height and significant decrease in fresh and dry weight which was associated with reduced photosynthetic O_2 evolution, photosynthetic pigments, chlorophyll fluorescence, and increased malondialdehyde (MDA) content (Rahimzadeh and Razavi, 2019). Cape gooseberry plants showed reduced plant height, leaf area, stem diameter, dry weight, root and reproductive organs, followed by yellowing, epinasty, necrosis and leaf abscission due to hypoxic conditions in the rhizosphere, under water logging stress condition (Aldana et al., 2014). Maize plants grown under waterlogging conditions significantly decreased the leaf area index (LAI), chlorophyll content, photosynthetic rate (P_n), photochemical efficiency (Φ PSII), and resulted in an increased MDA content ultimately causing deterioration of the membrane integrity (Ren et al., 2016). Deficiencies of Fe and P in strawberry plants led to a significant



reduction in shoot biomass, leaf size, chlorophyll content, affected the root exudate contents of galactaric acid, malic acid, lysine, proline, sorbitol-6-phosphate, dehydroascorbic acid, galactonate, and ferulic acid (Valentinuzzi et al., 2015). The deficiencies and toxicities of B and Zn in soybean plants affected the physiological processes and nutrient concentrations in the different plant tissues has been reported by Pawlowski et al. (2019).

PLANT GROWTH PROMOTING MICROBES

Endophytes

Plant endophytes grow inside healthy plant tissues but do not cause any harm or disease to the host plant. Some fungal endophytes promote plant growth despite environmental constraints (Yang et al., 2013). They play a vital role by supporting the host plant nutritionally through increased nitrogen, phosphorus, iron, etc., helps in defending the host plant from environmental stresses and aid in alleviating the stress antagonistic effects (Bacon and White, 2015; White et al., 2017).

The bacterial endophyte *Sphingomonas* sp. LK11 isolated from the leaves of *Tephrosia apollinea* alleviated salinity stress in wild-type and Got-3 tomato plants by significantly improving the shoot/root growth through the expression of peroxiredoxin-, glutathione S-transferase-, and glutaredoxin-related genes in LK11 genome (Khan et al., 2017). Rice plants inoculated with the root endophytic filamentous fungus, *Piriformospora indica*, showed significantly enhanced root / shoot lengths, fresh and

dry weights, increased photosynthetic pigment contents, which may be attributed to the increased proline accumulation which increased the plants stress tolerance to salinity (Jogawat et al., 2013). The application of encapsulated *Metarhizium brunneum* strain CB15 endophyte mitigated the nutrient deficiency by significantly enhancing the quantum yields of photosystem II (PSII), water use efficiency, plant biomass production, leaf area, nitrogen, and phosphorus contents in potato plants (Krell et al., 2018). Maize plants grown under drought stress conditions and inoculated with the endophytic fungus *Piriformospora indica*, a root-colonizing of Sebaciniales family, resulted in an increased root fresh and dry weight, leaf area, SPAD value, up-regulation of antioxidants such as catalase and superoxide dismutase. It also led to an increase in the proline content and a decline in the accumulation of malondialdehyde (MDA). The maize plants were able to mitigate the induced drought stress through up-regulation of drought-related genes *DREB2A*, *CBL1*, *ANAC072*, and *RD29A* (Xu et al., 2017).

Wheat plants infected with six endophytic fungi enhanced the efficiency of PSII, increased F_v/F_m values, increased plants height, seed weight, and seed germination rates under heat and drought stress conditions (Hubbard et al., 2014). The japonica rice plants inoculated with the fungal endophyte, *Paecilomyces formosus* LWL1, significantly improved plant growth attributes, such as plant height, fresh weight, dry weight, and chlorophyll content, increased protein content, grown under heat stress conditions. *P. formosus* LWL1 mitigated the heat stress in rice plants by down-regulation of the stress-related signaling molecules, abscisic acid

(ABA) and jasmonic acid (JA) (Waqas et al., 2015). Soybean plants infected with endophytic fungi *Paecilomyces formosus* significantly increased plant biomass and growth parameters, reduced lipid peroxidation, and accumulation of linolenic acid, GR, POX, CAT, and SOD under nickel (Ni) stress. This can be attributed to its phytohormonal synthesis and expression of *indole-3-acetamide hydrolase*, *aldehyde dehydrogenase* for indole-acetic acid and *geranylgeranyl-diphosphate synthase*, *ent-kaurene oxidase* (P450-4), *C13-oxidase* (P450-3) for gibberellins synthesis (Bilal et al., 2017). Under water stress conditions, capsicum plants inoculated with endophytic fungi *Penicillium resedanum* LK6 significantly increased the plant growth and yield parameters, peroxidase, catalase and polyphenol oxidase, capsaicin content which were attributed to the up-regulation of *Phenylalanine ammonia-lyase* and *Capsaicin synthase* genes activating the phenylpropanoid biosynthesis (Khan et al., 2014).

Arbuscular Mycorrhizal Fungi (AMF)

Symbiotic association of AMF helps the host plants to overcome various environmental stress conditions like pathogens, acidity, desiccation, and heavy metal toxicity by enhanced photosynthetic rate, water and nutrient uptake and leaf gas exchange (Zuccaro et al., 2009; Sun et al., 2018). AMF are broadly applied as biofertilizers in agriculture and more than 70% of the vascular plants can have a symbiotic association with AMF specifically under drought conditions by osmotic adjustment and enhanced antioxidant enzyme activity (Kohl et al., 2016; Wu and Zou, 2017). AMF colonization have the ability to enhance the uptake of macro-nutrients and micro-nutrients in plants leading to increased photosynthetic rate and biomass accumulation (Smith et al., 2003; Nell et al., 2010; Chen et al., 2017).

The cyclamen plants inoculated with AMF *Glomus fasciculatum* markedly enhanced biomass production, increased antioxidant enzymes activity like SOD, APX, as well as an increase in ascorbic acid and polyphenol contents which made the plants tolerant to heat stress conditions (Maya and Matsubara, 2013). Mathur et al. (2016) have reported that the maize plants colonized with AMF tolerated the high temperature stress by increased PSII active reaction centers, quantum efficiency of PSII, excitation energy trapping, performance index, net photosynthetic rate, and hence protecting the oxygen evolving complex (OEC). The AMF *Glomus etunicatum* protected the maize plants against low temperature stress conditions through improved water conservation (WC) and water use efficiency (WUE) which could play an indirect role in enhancing nutrient uptake, osmotic adjustment, the capacity of gas exchange and the efficiency of photochemistry of PSII (Zhu et al., 2010). AM fungus, *Glomus mosseae* alleviated the low temperature stress on tomato plants by reduced malondialdehyde (MDA) content, increased photosynthetic pigments, soluble proteins and antioxidant enzyme activities like SOD, POD, APX, and CAT (Abdel Latif and Chaouing, 2011). AMF can alleviate the heavy metal stress by any of the following mechanisms as reported earlier: (i) uptake and storing the heavy metals in the vacuoles of the fungi; (ii) adhering heavy metals to siderophores and sequester into the root apoplast or soil; (iii) catalyze the transport of heavy metals from cytoplasm through

transporters at the plasmalemma or tonoplast (Galli et al., 1994; Leyval et al., 1997; Schützendübel and Polle, 2002). Pigeon pea plants inoculated with the AMF *Glomus mosseae* under saline and cadmium (Cd) combined stress conditions enhanced the uptake of Cd, higher concentrations of stress metabolites (sugars, proteins, free amino acids, proline, and glycine betaine) and accumulation of phytochelatin thus enhancing growth, nutrient status, and yield of the host plant (Garg and Chandel, 2012).

Several reports are available that under drought stress conditions, AMF—host plant symbiotic association alleviated the stress effects by increased osmotic adjustment, proline accumulation, enhanced leaf gas exchange, leaf water relations, stomatal conductance, and transpiration rate (Morte et al., 2000; Kubikova et al., 2001; Mena-Violante et al., 2006; Yooyongwech et al., 2013). Tomato plants inoculated with (AM) fungus *Rhizophagus irregularis* and the plant growth promoting rhizobacteria (PGPR) *Variovorax paradoxus* 5C-2 alleviated the drought stress by enhanced photosynthetic activity, root hydraulic conductivity, and phosphorylation status (Calvo-Polanco et al., 2016). Sweet basil plants inoculated with AMF *Glomus deserticola* mitigated the reduction of K, P, and Ca uptake, improved photosynthetic efficiency, gas exchange, and water use efficiency under saline stress condition (Elhindi et al., 2017). A mycorrhizal consortium of *Glomus* sp., *Sclerocystis* sp., and *Acaulospora* sp., enhanced the salt tolerance of date palm plants grown under saline conditions through improved Ca/Na and K/Na ratios, enhanced concentrations of photosynthetic pigments and protein content, increased activities of antioxidant enzymes (SOD, CAT, POD, and APX) (Ait-El-Mokhtar et al., 2019). Sheng et al. (2011) have reported that the AMF *Glomus mosseae* inoculation has enhanced the accumulation of soluble sugars, reducing sugars, soluble protein, total organic acids, oxalic acid, fumaric acid, acetic acid, malic acid, and citric acid, subsequently enhancing the up-regulation of osmoregulation process in the host maize plants grown under salinity stress condition. Citrus seedlings inoculated with a mixture of AM fungi (*Rhizophagus irregularis* and *Funneliformis mosseae*) inhibited the uptake of Na or Cl while favoring the uptake of P, K, Fe, and Cu under saline condition (Navarro et al., 2014). Tomato plants inoculated with *Scolecobasidium constrictum* alleviated the combined drought and salinity stress condition by enhanced biomass production, leaf water relations, stomatal conductance, and F_v/F_m (Duc et al., 2018).

Plant Growth-Promoting Rhizobacteria (PGPR)

PGPR are microorganisms that successfully colonize plant roots and positively enhance plant growth, after been inoculated on seeds. Rhizosphere is the area surrounding a plant root that is inhabited by a distinctive microbial population which are influenced by root exudates like organic acids, amino acids, proteins, sugar, phenolics, and other secondary metabolites (McNear, 2013). The symbiotic relationship between N-fixing rhizobia and legumes has been extensively studied wherein the legumes provide reduced carbon (C) to the rhizobia and in turn, biologically available N is provided by the rhizobia to the

legumes. The legume develops root nodules, to host the rhizobia and the rhizobia changes from rod-shaped cell to branched, N-fixing bacteroid (Oke and Long, 1999).

PGPRs are able to synthesize phytohormones such as IAA, gibberellins, ethylene, abscisic acid and cytokinins that help the plants to become tolerant various abiotic environmental stresses. Inoculation of PGPR helps in increased plant dry biomass, grain production, and flowering, which can be related to increase in root development, further enhancing the water and mineral uptake by the host plant roots (Okon et al., 1998). Certain bacteria such as *Azospirillum*, *Bacillus*, *Burkholderia*, *Erwinia*, *Pseudomonas*, *Rhizobium*, or *Serratia* have been reported as phosphate solubilizing bacteria which helps in increasing the biological nitrogen fixation efficiency, improve the availability of Fe and Zn, and alter the growth of roots or shoots by production of plant hormones (Kucey et al., 1989; Mehnaz and Lazarovits, 2006). Potassium-solubilizing bacteria/fungi have been isolated from rhizosphere soil of different crops, which cause solubilization of potassium by the production of organic/inorganic acids or polysaccharides (Sindhu et al., 2016). PGPR plays a vital role in plant growth and development under stressful conditions through different mechanisms like fixation of nitrogen, solubilization of phosphorus, zinc solubilization, siderophores production, growth regulators, organic acids, enzymes like ACC-deaminase, chitinase, and glucanase (Glick et al., 2007; Berg, 2009; Hayat et al., 2010; Kamran et al., 2017).

Phytohormones are molecular signals (auxin, cytokinin, gibberellic acid, brassinosteroids, ethylene, abscisic acid, salicylic acid, and jasmonic acid) that play a crucial role in plant growth and development, and are expressed in response to environmental stress factors (Fahad et al., 2015). Many PGPR can produce auxins (Omer et al., 2004), gibberellins (Jha and Saraf, 2015), and cytokinins (Ruzzi and Aroca, 2015) which lead to enhanced plant shoot growth and root exudate production. PGPR has the ability to synthesize indole acetic acid (IAA), an important hormone of auxin class, helps in the regulation of differentiation of vascular tissue, differentiation of adventitious and lateral root, cell division, and shoot growth under drought stress conditions (Goswami et al., 2015). Maize plants inoculated with PGPR ameliorated drought stress by enhancing the abscisic acid (ABA) concentration levels, regulating transcription of drought related gene and root hydraulic conductivity (Jiang et al., 2013). Soybean plants inoculated with *Pseudomonas putida* H-2-3 mitigated salinity and drought stress by increased chlorophyll content, enhanced shoot length and biomass, enhanced the abscisic acid and salicylic acid, polyphenol, flavonoids, SOD and 2,2-diphenyl-1-picryl-hydrazyl-hydrate (DPPH) scavenging activity (Kang et al., 2014).

Under salinity stress condition, lettuce seeds inoculated with *Azospirillum* showed better seed germination and vegetative growth (Barassi et al., 2006). Tolerance to salinity stress has been exhibited by two bacterial strains, *Bacillus aryabhatai* H19-1 and *Bacillus mesonae* H20-5 in tomato plants by enhancing ABA levels, accumulating significant levels of proline, abscisic acid (ABA), and antioxidant enzyme activities which might be attributed by the up-regulation of *9-cisepoxycarotenoid dioxygenase 1 (NCED1)* and *abscisic*

acid-response element-binding proteins 1 (AREB1) genes (Yoo et al., 2019). Qiyuan et al. (2016) have reported that the rhizobacterium *Variovorax paradoxus* 5C-2 mitigated salinity stress in pea plants by the secretion of 1-aminocyclopropane-1-carboxylase (ACC) deaminase, which helped in improving water relations, ion homeostasis, reduced ethylene production and photosynthesis. Wheat plants inoculated with *Piriformospora indica* and *Azotobacter chroococcum* significantly increased shoot and root biomass, photosynthetic pigment contents, decreased malondialdehyde (MDA) content, increased ascorbate peroxidase (APX) and peroxidase (POD) activity, and alleviated the Zn deficiency conditions. The enhanced zinc uptake might be one of the major mechanisms to improve the wheat plants to cope with Zn deficiency (Abadi and Sepehri, 2015).

TOLERANCE MECHANISMS BY PLANT-MICROBE INTERACTION

Endophytes exhibit a symbiotic association residing within the plant for the majority of their life cycle and has the ability to colonize plant's internal tissues by entering into the seed, leaf, stem, and root of a host plant. Endophytes help in nitrogen fixation, secrete phytohormones and nutrient acquisition thus improving plant growth. Plants do produce root exudates which acts as the energy source for endophytic microorganism associated with it (Kandel et al., 2017; Shen et al., 2019). During the early stages of endophytic colonization, the bacterial cells synthesize exopolysaccharides (EPS) which facilitate its attachment onto the root surface and also protects the bacterial cells from oxidative damage (Meneses et al., 2011). Arbuscular mycorrhizal fungi are soil-borne fungi that can significantly enhance plant nutrient acquisition and tolerant to various abiotic stress conditions. The AMF establishes a symbiotic association with its host plant, regulating the growth and development of plants. The AMF mycelial network extends under the roots of the plant, hence promoting nutrient uptake. The common mycorrhizal network (CMN) has a profound effect on the fungal-mediated transport of phosphorus (P) and nitrogen (N) to plants and hence support plant development under stressful environmental conditions (Navarro et al., 2014; Sun et al., 2018).

Through plant-microbe interaction, microbes use various biochemical and molecular mechanisms which help in mitigating the negative impact of various abiotic stress on plant growth and development (**Figure 1** and **Table 1**). Phytohormones like auxins, gibberellins and cytokinins play a major role in changing the root morphology, thus enabling the plants to get adapted and tolerant to various abiotic stresses like salinity, heavy metal, drought and nutrient deficiency. Secretion of auxins such as indole acetic acid (IAA) enhances cell elongation, resulting in enhanced root growth, promotes lateral root development and hence, has a positive effect on water acquisition and nutrient uptake by the plants. Plant growth promoting rhizobacteria (PGPR) helps to mitigate the negative impact of abiotic stress through induced systemic tolerance (IST) which includes: (i) production of phytohormones such as indole-3-acetic acid (IAA), cytokinins and abscisic acid (ABA), (ii) production of antioxidants like

TABLE 1 | Microbial mediated abiotic stress tolerance.

Plants	Microbes	Stress	Tolerance mechanism	References
<i>Panicum turgidum</i>	<i>Funnelformis mosseae</i> <i>Rhizophagus intraradices</i> <i>Claroideoglossum etunicatum</i>	Salinity	Increased chl <i>a</i> , chl <i>b</i> , carotenoids, increased antioxidant enzyme activities like SOD, POD, CAT, and GR, increased uptake of essential elements like phosphorous, potassium, and calcium	Hashem et al., 2015
<i>Cucumis sativus</i> , cv. Dasher II	Arbuscular mycorrhizal fungi	Salinity	Synthesis of pigments, activity of antioxidant enzymes, including SOD, CAT, APX, GR, and ascorbic acid, accumulation of phenols and proline, jasmonic acid, salicylic acid, and several important mineral elements (K, Ca, Mg, Zn, Fe, Mn, and Cu) were enhanced	Hashem et al., 2018
<i>Pisum Sativum</i> L.	<i>Rhizoglossum intraradices</i> , <i>Funnelformis mosseae</i> , <i>Rhizoglossum fasciculatum</i> and <i>Gigaspora</i> sp.	Salinity	Higher nutrient uptake, accumulation of compatible osmolytes, and lower cellular leakage of electrolyte	Parihar et al., 2020
<i>Zea mays</i> L.	<i>Kocuria rhizophila</i>	Salinity	Regulating plant hormones (IAA and ABA) levels and improving nutrient acquisition, higher transcript levels of genes encoding antioxidants (<i>ZmGR1</i> and <i>ZmAPX1</i>), and genes involved in salt tolerance (<i>ZmNHX1</i> , <i>ZmNHX2</i> , <i>ZmNHX3</i> , <i>ZmWRKY58</i> , and <i>ZmDREB2A</i>)	Li et al., 2020
<i>Robinia pseudoacacia</i> L.	<i>Funnelformis mosseae</i> <i>Rhizophagus intraradices</i>	Lead (Pb)	Higher gas exchange capacity, non-photochemistry efficiency, and photochemistry efficiency, enhanced superoxide dismutase (SOD), ascorbate peroxidases (APX), and glutathione peroxidase (GPX)	Yang et al., 2015
<i>Helianthus annuus</i> L.	<i>Funnelformis mosseae</i> <i>Rhizophagus intraradices</i> <i>Claroideoglossum etunicatum</i>	Cadmium (Cd)	Increase in shoot/root fresh and dry weight, chl <i>a</i> , chl <i>b</i> , carotenoids, antioxidant enzymes like SOD, POD, CAT, GPX, and GR, decreased fatty acid content	Abd_allah et al., 2015
<i>Glycine max</i> L.	<i>Paecilomyces formosus</i>	Heavy metals (Ni, Cd, and Al), drought, high temperature	Enhanced glutathione, catalase, and SOD activities, decreased lipid peroxidation, enhanced macronutrient uptake, down-regulating heavy metal ATPase gene, up-regulation of drought-related and heat shock protein genes	Bilal et al., 2020
<i>Poncirus trifoliata</i>	<i>Glomus versiforme</i>	Iron (Fe)	Promoted growth and phenolic synthesis, increase in phenylalanine ammonia-lyase activity (PAL) enzyme activity and <i>pa1</i> gene expression	Li et al., 2015
<i>Nicotiana tabacum</i> L. cv Petit Havanna	<i>Rhizophagus intraradices</i>	Phosphorus (P) deficiency	Decreased rate of root respiration and exudation of citrate and malate	Del-Saz et al., 2017
<i>Sorghum bicolor</i> L.	<i>Glomus intraradices</i> , <i>Glomus mosseae</i> , <i>Glomus aggregatum</i> , <i>Glomus etunicatum</i>	Iron (Fe) deficiency	Increase in phytoalexin, upregulation of <i>SbDMAS2</i> (deoxymugineic acid synthase 2), <i>SbNAS2</i> (nicotianamine synthase 2), and <i>SbYS1</i> (Fe-phytoalexin transporter yellow stripe) in roots, enhanced S-containing antioxidant metabolites (Met, Cys, and GSH) as well as enzymes (CAT, SOD, and GR)	Prity et al., 2020
<i>Cucumis sativus</i> L. cv. Zhongnong No. 26	<i>Rhizophagus irregularis</i>	Low temperature	Improved phosphorus (P) uptake, induced of P _i transporter gene belonging to the <i>Ph1</i> gene family	Ma et al., 2015

(Continued)

TABLE 1 | Continued

Plants	Microbes	Stress	Tolerance mechanism	References
<i>Solanum lycopersicum</i> L. cv. Zongza 9	<i>Funnelformis mosseae</i>	Low temperature	Reduced level of MDA, H ₂ O ₂ , and O ₂ ⁻ , induced activities of antioxidant enzymes APX, MDHAR, GR, and DHAR, expression levels of APX, MDHAR, GR, and DHAR genes	Liu et al., 2015
<i>Solanum melongena</i> L.	<i>Funnelformis mosseae</i> , <i>Claroideoglomus etunicatum</i> , <i>Rhizophagus irregularis</i> , and <i>Diversispora versiformis</i>	Low temperature	Improved photochemical reactions, activating antioxidant defense systems, accumulating protecting molecules, and reducing membrane damages	Pasbani et al., 2020
<i>Colobanthus quitensis</i>	Fungal endophytes	UV-B Radiation	Expression of genes associated to UV-B photoreception, accumulation of flavonoids	Barrera et al., 2020
<i>Solanum lycopersicum</i> cv. ACE 55	<i>Fusarium solani</i>	Water	Increased net CO ₂ assimilation rate (P _N), stomatal conductance (g _s), leaf relative water content (RWC), and maximum potential quantum yield of PSII, enhanced antioxidant enzyme activities like SOD, POD, APX, and CAT, decreased oxidative membrane damage	Kavroulakis et al., 2018
<i>Triticum aestivum</i>	<i>Rhizophagus intraradices</i> , <i>Funnelformis mosseae</i> , <i>Funnelformis geosporum</i>	Drought	Increased RWC, maximum photochemistry, higher Chl content, restoration of electron transport in PSII, higher P _{I(ABS)} , PSI photochemistry	Mathur et al., 2018
<i>Zea mays</i> L.	<i>Glomus versiforme</i>	Drought	Improved chlorophyll content, mineral uptake and assimilation, increased content of compatible solutes, such as proline, sugars, and free amino acids, Up-regulation of the antioxidant system	Begum et al., 2019
<i>Cicer arietinum</i> L.	<i>Bacillus subtilis</i> , <i>Bacillus thuringiensis</i> and <i>Bacillus megaterium</i>	Drought	Increased leaf proline content, activities of antioxidant enzymes (CAT, APOX, POD, and SOD), significant accumulation of riboflavin, L-asparagine, aspartate, glycerol, nicotinamide, and 3-hydroxy-3-methylglutarate	Khan et al., 2019
<i>Triticum aestivum</i> and <i>Zea mays</i>	<i>Bacillus</i> sp. and <i>Enterobacter</i> sp.	Drought	Production of indole-3-acetic acid (IAA) and salicylic acid (SA)	Jochum et al., 2020

SOD, POD, APX, CAT, GR, and (iii) degradation of the ethylene precursor ACC by bacterial ACC deaminase (Farooq et al., 2009; Porcel et al., 2014). Inoculating plants with PGPR containing 1-aminocyclopropane-1-carboxylate (ACC) deaminase enzyme, can help to mitigate abiotic stresses by regulating the ethylene production by metabolizing ACC (an immediate precursor of ethylene biosynthesis) into alpha-ketobutyrate and ammonia (Saleem et al., 2007). Microbes do have the capability to promote plant growth and development under abiotic stress condition by enhancing the production of low-molecular-weight osmolytes, including glycinebetaine, proline and other amino acids, organic acids, nitrogen fixation, mineral phosphate solubilization and producing key enzymes such as ACC-deaminase, chitinase, and glucanase (Ahmad et al., 2011; Gupta et al., 2013). Microbes have enhanced heavy metal tolerance through transportation across cell membrane, accumulation on cell wall, intra as well as extracellular entrapment, formation of complexes and redox reactions (Nanda et al., 2019). Arbuscular mycorrhizal fungi

(AMF) play an important role in mitigating the abiotic stresses through various mechanisms like increased osmotic adjustment, enhanced accumulation of proline, increased glutathione level, down regulation of stress related genes, enhanced synthesis of jasmonic acid, salicylic acid, several important inorganic nutrients and expression of stress resistance genes to enhance the defense system (Kubikova et al., 2001; Ouziad et al., 2005; Lim and Kim, 2013; Yooyongwech et al., 2013; Hashem et al., 2018).

CONCLUSION

The various abiotic stresses pose a major threat to world food security by exerting their deleterious effects on the crop growth, physiological and biochemical plant functions, and ultimately affecting the crop yield. Of the various strategies adapted by the plants to tolerate the abiotic stresses, the plant-microbe interactions provide an efficient eco-friendly manner in which the plants can cope up with the adverse

environmental stress conditions. The microbial consortium present in the root microbiome promotes plant growth by regulating phytohormones synthesis, osmolytes, organic acids, improved nutrition uptake, enhanced antioxidant system, and up-regulation of stress tolerant genes. However, further studies are required at molecular level to understand the exact mechanism of stress tolerance imparted by the various microbial community. Moreover, the search for even more potential stress tolerant microbes and application of those microbial consortia

on field conditions has to be extensively researched in the future which will be of prime importance in solving the future food security worldwide.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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Conflict of Interest: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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