Physiological and Biochemical Responses in Maize under Drought Stress

Suphia Rafique

1 Introduction

Global warming led to rise in temperatures and severe water scarcity or drought stress, which drastically hamper plant growth, development, and yield every year in major crops of the world. Mostly, the drought obstructs plant growth and development and reduces biomass accumulation (Farooq et al. 2009). The other main consequences of drought stress are reduction in CO_2 assimilation rate (Kaiser 1987), reduced chlorophyll content (Rong-hual et al. 2006), reduction in leaf size due to reduced cell expansion and cell division (Verelst et al. 2013; Tardieu et al. 2000) and stomatal closure (Cochard 2002), and low water use efficiency (WUE) (Hatfield and Dold 2019). The other massive physiological changes in plants are reduction in shoot growth (Pace et al. 1999), delayed flowering time (Pantuwan et al. 2002; Angus and Moncur 1997; Dwyer and Stewart 1987), and fresh/dry weight (Liu et al. 2011). Drought also affects crop phenology (Bindiger et al. 1987) and induces early transition from the vegetative to the reproductive phase (Desclaux and Roumet 1996) leading to altered crop growth cycle. The essential phytohormone abscisic acid (ABA), which is generated in response to drought stress and is crucial for plants to respond to stress (Yamaguchi-Shinozaki and Shinozaki 2006; Cui et al. 2017), increased ABA level leads to stomatal closure (Wilkinson and Davies 2010) and prevent water loss, and increase water use efficiency (Chaves et al. 2009)thus water deficiency signals perceived by ABA receptors (PYR/RCAR) (He et al. 2018). As the plants received the water deficiency signals, it initiates the physiological and biochemical adaptation strategies. The drought resistance mechanism can be grouped into three categories: (i) drought escape (complete life cycle before drought affects its survival), (ii) drought avoidance (endurance with increased internal water

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S. Rafique (✉)
Department of Biotechnology, Faculty of Chemical and Life Sciences, Jamia Hamdard,
New Delhi, Delhi, India

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content and preventing tissue damage), and (iii) drought resistance (endurance with low internal water content, whereas sustaining growth over the drought period) (Maiti and Satya 2014; Bänziger et al. 2000; Song et al. 2016). Therefore, the first cellular water loss by drought stress promotes the drought signals to produce stress-protected metabolites such as proline, trehalose, sugars, and alcohols and also triggers production of enzymatic antioxidant system (CAT, SOD, ascorbic peroxidase) and nonenzymatic antioxidant (vitamin C, glutathione, and tocopherols) to prevent acute cellular damage and to maintain membrane integrity and redox homeostasis (Mittler 2002; Ashraf 2009; Halimeh et al. 2013; Waseem et al. 2015; Kosar et al. 2015). Wheat, rice, and maize are the three primary crops grown globally (FAOSTAT 2010). Maize usually requires 500–800 mm during life cycle (Critchley and Klaus 1991). The main effect of water scarcity throughout its life cycle is to reduce its water and *N* use efficiencies, resulting in substantial yield losses (Ashraf et al. 2016). Heisey and Edmeades (1999) estimated that 20–25% of the global maize planting area is affected by drought yearly. In maize, grain yield reduction caused by drought ranges from 10% to 76% depending on the severity and stage of occurrence (Bolaños et al. 1993). All vegetative and yield parameters were significantly affected by water shortage. At vegetative growth period, short-duration water deficits caused 28–32% loss of final dry matter weight. In a similar way, single irrigation omission during tasselling and cob formation stages (sensitive stages) may cause 30% and 40% grain yield loss during dry years (Cakir 2004). As the water availability decreases, the biomass production also decreases. Kamara et al. (2003) revealed that water deficit imposed at various developmental stages of maize reduced total biomass accumulation at silking by 37%, at grain-filling period by 34%, and at maturity by 21%. Thus, drought stress severely hampers the growth and productivity of maize (Liu et al. 2010; Ge et al. 2012; Talaat et al. 2015). It triggers different changes in crop plants through various morphological, physiological, and biochemical responses (Ahammed et al. 2020; Jan et al. 2019; Hussain et al. 2020). Anjum et al. (2011a) indicated that drought stress in maize led to considerable decline in net photosynthesis (33.22%), transpiration rate (37.84%), stomatal conductance (25.54%), water use efficiency (50.87%), intrinsic water use efficiency (11.58%), and intercellular CO2 (5.86%) as compared to control plants. Adverse conditions in maize plants evoked various mechanisms to deal with the stressful environment such as antioxidant capabilities, osmotic adjustment, reduction in photosynthetic rates, and ABA accumulation (Gong et al. 2014; Sah et al. 2016). The varied physiological, morphological secondary traits have been identified for improving the drought tolerance in maize (Edmeades et al. 1997; Bänziger et al. 2000; Monneveux et al. 2008). Thus, drought-associated physiological and metabolic modifications could be used as stress indicators for measuring the susceptibility or tolerance of a plant in response to water stress environments (Alharby and Fahad 2020). This chapter contains information on physio-biochemical aspects of drought tolerance mechanism of maize crop in particular. The maize leaves have special anatomy (Kranz anatomy), the PCR cycle is operative in bundle sheath (BS) chloroplast, and PCR cycle enzymes are very sensitive to H_2O_2. The Bundle Sheath tissues sustain the majority of the oxidative damage due to insufficient antioxidant defense in this tissue. The drought affects the vegetative and reproductive phase. However, after drought, stress recovery periods play an important role in drought adaptation. The effects of drought stress can be reduced through priming and application of beneficial microorganism. However, in present climate change scenario and for long-term food security, there is a need to develop the crop varieties which can sustain growth and sustainable production in drought conditions.

2 Morpho-physiological Changes Under Drought Stress

Drought stress affects the morpho-physiology of maize at both the cellular and whole-plant levels. The primary effects of drought include decreased plant height, reduced leaf elongation, and induced leaf withering (Habben et al. 2014), perturb root system, leaf rolling, reduction in photosynthetic rate, stomatal conductance, assimilate translocation, all these reduced growth rate and plant dry biomass (Bänziger et al. 2000; Yin et al. 2010; Zhang et al. 2011). Maize crop is extremely sensitive to drought stress (Farre et al. 2000). Early studies exhibited that the various morpho-physiological characteristics showed distinctive responses to drought stress, such as root development, stomatal activity, osmotic adjustment, abscisic acid, and proline levels in the whole plant (Li and Van Staden 1998a, b; Selmani and Wasson 2003). In a study of eight maize cultivars, drought stress significantly decreased shoot fresh and dry weights, root fresh and dry weights, and chlorophyll pigments (*a* and *b*) (Shafiq et al. 2019). The proportional decrease of shoot biomass was greater than the proportional decrease in root biomass, leading to an increase in the root/shoot ratio as water deficit stress increased at all growth stages (Benjamin et al. 2014). In six different maize hybrids under drought stress, drought affects plant height and chlorophyll content (except for one NPE4) and causes a rise in leaf temperature in all hybrids (Witt et al. 2012). On comparing the two cultivars for growth response and some physiological characteristics, O'Regan et al. (1993) observed that drought-resistant cultivar had a higher growth rate and deeper rooting, higher transpiration rate and lower diffusive resistance during the onset of water stress, and higher relative water content and levels of abscisic acid and proline throughout the period of water stress than the drought-sensitive cultivar. In maize, water deficit shows clearly a concerted downregulation of NR activity and photosynthesis (Foyer et al. 1998).

2.1 Priming Improved Physiological Process

Priming is one of the most important physiological methods which improves the seed performance and provides faster and coordinated germination (Nawaz et al. 2013). The seeds have been primed to reduce the time between seed sowing and seedling emergence, thus to synchronize emergence processes (Parera and Cantliffe

1994). However, the response of tolerant and sensitive maize cultivars was not remarkable differentiae when foliar spray of α-tocopherol (0 mmol and 50 mmol) at vegetative stage on two maize cultivars (Agaiti-2002 and EV-1098) improved the growth of both cultivars, besides improvements in photosynthetic pigment, water relations, antioxidative mechanism, and better nutrient acquisition in root and shoot along with tocopherol contents and a decrease in lipid peroxidation (Ali et al. 2020). Furthermore, after foliar application, the tocopherol level increases in roots because of basipetal translocation and thus induction of drought tolerance of maize associated with tissue-specific improvements in antioxidative defense mechanism through its translocation. Likewise, the seedlings of a drought-tolerant (NK8711) and drought-sensitive (P1574) maize hybrid were foliar sprayed with various SNP (sodium nitroprusside) doses (0, 50, 100, 150, and 200 μM) under drought stress conditions. Foliar spray of 100 μM markedly improved water status and chlorophyll contents and alleviated drought-induced oxidative damages through increased antioxidant (catalase, ascorbate peroxidase, and superoxide dismutase) activities in both maize hybrids (Majeed et al. 2018), whereas maize seed presoaking in ascorbic acid (AsA) or salicylic acid (SA) solutions resulted in massive increase in growth parameters, chlorophyll contents, osmo-protectants (soluble sugars, free amino acids, and soluble proteins), antioxidant enzyme activity [ascorbate peroxidase (APOX) and superoxide dismutase (SOD)], and nonenzymatic antioxidants [carotenoids and glutathione (GSH)] content as compared to control. Conversely, proline, catalase (CAT), and malondialdehyde (MDA) content were decreased significantly (Loutfy et al. 2020). Application of melatonin with the root-irrigation method and the leaf-spraying method on maize seedlings improved the photosynthetic activities and alleviated the oxidative damages under the drought stress. Compared with the leaf-spraying method, the root-irrigation method was more effective on enhancing drought tolerance (Huang et al. 2019). In contrast, some of the studies indicated distinct response of tolerant and susceptible genotypes on pretreatment of seeds. Two maize cultivars drought resistance PAN (6043) and drought sensitive (SC 701) in different concentrations of uniconazole, brassinolide, and methyl jasmonate enhanced and maintained a higher relative water content and diffusive resistance and decreased the relative conductivity and transpiration rate in the seedlings of the drought-resistant cultivar, PAN 6043, whereas treatments have the opposite effect on seedlings of the drought-sensitive cultivar (which decreased the relative water content) (Li and Van Staden 1998a, b). In maize, the bio-stimulant *Kappaphycus alvarezii* seaweed extract (KSWE) was applied foliarly only once at the grain-filling stage in moderate and severe stress. There was lesser degree of oxidative stress in KSWE-treated plants. There is a decrease in lipid peroxidation and increase in activities of antioxidant enzymes and nonenzymatic antioxidant like GSH (glutathione) and proline (Trivedia et al. 2018).

2.2 Effect of Drought and Recovery Period on Maize

Plant responses to water scarcity are complex processes; plants either involve in adaptive changes or have a deleterious effect. It also depends on the intensity and duration of stress as well as plant species and the stage of development (Chaves et al. 2003). The physiological responses of the maize (*Zea mays* L.) cultivars (Doge, Vero and Luce) to drought stress and recovery were determined. Growth of all cultivars was retarded under drought stress conditions and regained speed during the recovery stage. Although many physiological parameters decrease (FM, FV/FM, FV′/FM′, ϕPSII and qL, and an increase of non-photochemical quenching (NPQ)), they regain in all the three cultivars after recovery period except in Doge, although Doge has the ability to withstand drought with better upregulating its protective mechanisms such as increasing NPQ, chla/b ratio (smaller antenna size), and anthocyanin and proline content decreasing FV′/FM′ compare to other two cultivars. As a result of that, Doge was classified as less drought tolerant but others as tolerant (Efeoglu et al. 2009). Further, natural gradual drought stress was applied to maize inbred lines, and seedlings were observed for growth and various physiological responses for drought stress and recovery. Drought induced decrease in all the physiological parameters (leaf water content, water potential, osmotic potential, gas exchange parameters, chlorophyll content, Fv/Fm and nitrogen content, and increased H2O2 accumulation and lipid peroxidation). However, after recovery, most of these physiological parameters rapidly returned to normal levels. Although drought resistance-related parameters were leaf water potential and chlorophyll content while chlorophyll content and Fv/Fm were associated with drought recovery, hence, drought recovery and drought resistance are the major causes of maize seedling drought adaptation. In addition, leaf water potential, chlorophyll content, and Fv/Fm could be used as efficient reference indicators in the selection of drought-adaptive genotypes (Chen et al. 2016). Likewise maize (*Zea mays* L.) plants of two inbred lines were subjected to two cycles of drought and rewatering. Metabolic pathways in the maize plants returned to their normal status at different rates during recovery. The results provide valuable insight into the growth, biochemical, and metabolic mechanisms used by maize to adapt to cyclic drought (Sun et al. 2016). Also growth limitation depends on the number of drought cycles and either full or partial recovery of growth. Moreover, to overcome from cyclic drought stress, maize plants adjusted their leaf spectral properties and employ growth and biochemical strategies and recover from drought stress after rewatering. However, the extent of plant growth recovery after rewatering may depend on plant genotype and the number of consecutive drying cycles (Sun et al. 2018).

2.3 Physiological Changes in Vegetative/Reproductive Phase Under Drought

Several reports have shown that water demand of maize crop is less at early vegetative growth (Shaw 1977; Cakir 2004). However, Cakir (2004) explained that water deficit decline in plant extension growth and reduction of leaf size at vegetative stage reduced the grain yield up to 40%. Maize hybrids with higher levels of antioxidant enzyme activities both at vegetative and reproductive stages showed higher resistance to drought stress and produced higher yield under stress (Ghahfarokhi et al. 2016). The reproductive stage of maize has higher water requirement (Kranz et al. 2008); water stress just before anthesis, during silking and seed filling periods, reduces the yield potential (NeSmith and Ritchie 1992; Cakir 2004; Musick and Dusek 1980; Moser et al. 2006). The drought stress relied on drought intensity and duration, with more severe drought stress creating more serious effects on maize. The responses of maize (*Zea mays* L.) in different water deficit conditions were examined; the moderate stress during the silking and blister stages has no significant change in the relative water content (RWC) but significant changes in the relative conductivity (RC) of the leaves. However, severe stress significantly decreases the leaf RWC and increases membrane permeability (leaf relative conductivity). Furthermore, under severe drought stress, antioxidant enzyme activities declined significantly in later stages, namely, for superoxide dismutase (SOD) during the tasseling and blister stages, for peroxidase (POD) during the milk stage, and for catalase (CAT) during the tasseling, blister, and milk stages. Meanwhile, membrane lipid peroxidation (measured as malondialdehyde content) significantly increased in all stages (Bai et al. 2006). A transgenic maize plant with increased ZmNFYB2 expression shows tolerance to drought based on the responses of a number of stress-related parameters, including chlorophyll content, stomatal conductance, leaf temperature, reduced wilting, and maintenance of photosynthesis. These stress adaptations contribute to a grain yield advantage to maize under water-limited environments (Nelson et al. 2007). Mansouri-Far et al. (2010) evaluated the yield response of two maize hybrids at vegetative and reproductive stage under water stress and normal conditions. Water stress minimized the characteristics such as leaf greenness, relative water content, grain yield, and 100 kernel weight but maximized proline content; 100 kernel weight was considered highly sensitive to water stress. Bolaños et al. (1993) emphasize the importance of secondary traits in increasing selection efficacy for grain yield under severe drought stress during eight cycles of recurrent full-sib selection in the lowland tropical maize *(Zea mays* L.) population. Secondary traits like increased relative stem and leaf elongation rate (REL), delayed foliar senescence, reduced canopy temperatures, and reduced ASI increased efficacy of selection for grain yield under drought. However, Bruce et al. (2002) in their review article emphasized that reproductive success can be achieved through better partitioning of biomass to the developing ear results in faster spikelet growth; this in turn reduced the number of spikelet formed on the ear that facilitates overall seed set by reducing carbon and water constrains per spikelet. Multiple, independent transgenic hybrids (transgenic gene-silencing approach was used to modulate the levels of ethylene biosynthesis in maize (*Zea mays* L.)) were tested in field trials at managed drought stress- and rain-fed locations for its effect on grain yield. The yield performance in transgenic hybrids had significantly increased with a 0.58 Mg/ha (9.3 bushel/acre) increase after a flowering period drought stress, whereas analysis of secondary traits showed that there was a consistent decrease in the anthesis silking interval and a concomitant increase in kernel number/ear in transgenes (Habben et al. 2014). A drought-resistant maize plant is characterized by reduced plant height, smaller tassels, smaller leaves above the ear, erect leaves, larger stem diameter, stay-green, and deeper rooting with less lateral branching and less root biomass, compared to a drought-susceptible phenotype (Ribaut et al. 2008).

3 Biochemical Changes Under Drought Stress

3.1 Metabolic Changes and Oxidative Defense Mechanism for Drought Tolerance

Maize plant most sensitive to drought stress is often used as model crop to assess the impact of drought tolerance (Anjum et al. 2011a). In C4 plants, the antioxidative enzymes are distributed between mesophyll and bundle sheath cells (Foyer 2002), whereas H2O2 was found to accumulate only in mesophyll cells (Doulis et al. 1997). Perhaps the PCR cycle is operative in bundle sheath chloroplast, and enzymes of PCR cycle are very sensitive to H2O2; thus, it is suggested that oxidative damage under stressful conditions in C4 plants is restricted to bundle sheath tissue because of inadequate antioxidant protection in this tissue (Kingston-Smith and Foyer 2000). The key reaction of plants in drought stress is the production of reactive oxygen species (ROS) such as superoxide, hydroxyl radicals, hydrogen peroxide, and singlet oxygen (Jiang and Zhang 2004; Ashraf 2009; Ali and Ashraf 2011). A study shows maize cultivars under water deficit conditions (eight maize cultivars) significantly increased free proline, glycinebetaine (GB), total phenolics, hydrogen peroxide (H2O2), malondialdehyde (MDA) contents, activities of enzymatic antioxidants (CAT, POD, and SOD), and ascorbic acid (AsA) contents (Shafiq et al. 2019). Some recent work have been cited in Table 1. Further, Chugh et al. (2011) reported drought-tolerant genotypes LM5, and Prakash exhibits the effective antioxidant defense mechanism which is capable to quench H2O2 and superoxide radicles. Also, these genotypes accumulate less MDA and H2O2, together with high ascorbic acid content during stress conditions. These ROS cause oxidative damage to membrane lipid structure, DNA, and proteins (Nair et al. 2008; Ashraf 2009, Anjum et al. 2011a), while tolerant plants accumulate less MDA (malondialdehyde) and increase the regulation of antioxidant enzymes (Teisseire and Guy 2000; Zhang et al. 2007). Similarly, Anjum et al. (2016) examine two maize cultivars (Rung Nong 35 and Dong Dan 80) under progressive drought stress. Higher tolerance to drought stress

Table 1 Physio-biochemical responses of maize genotypes in drought stress during the period from 2018 to 2021

Maize genotypes	Stress stage	Physio-biochemical response	Reference
B_{73} and MO_{17}	27 days before flowering	Increase activity of SOD, CAT, GB, proline, and MDA. Enzymatic and nonenzymatic antioxidant and organic osmolytes increase significantly in both lines. SOD activity and GB and proline content are potential biochemical indicators of drought resistance MO_{17} line	Moharramnejadet al. (2019)
Tolerant cultivar (Karoon) and susceptible (260)		Increase in root growth indices, H2O2 content, and antioxidant enzyme activity. Tolerant cultivars increase polyamine oxidase activity and putrescine synthesis rate.	Ahangir et al. (2020)
B104 line	Vegetative and reproductive	Higher photosynthesis rate, antioxidant enzyme activity, better membrane stability, and less electrolyte leakage	Wang et al. (2018)
Drought-tolerant (Chang 7-2) and sensitive (TS141) varieties	Seedling roots	Tolerant variety strong water retention capacity, synergistic effect of antioxidant enzymes, strengthened cell wall, osmotic stabilized PM proteins, effective recycling amino acid, and improved lignification	Zeng et al. (2019)
Madura local maize variety	Germinating stage	Higher antioxidant capacities (ABTS), hydroxyl radical scavenging and antioxidant enzyme CAT and APX activities. All plays an important role in germination phase	A. R. H Dani and T. A. Siswoyo
Hybrid Shaanke 9	At sixth leaf stage	Mild stress adaptive response-activation antioxidant system and photorespiration Severe stress damage photosynthetic apparatus	Li et al. (2021)
Hybrid Xida 889 and Xida 319	At tasseling stage 15 days	Xida 889 greater tolerance, strong antioxidant defense system, osmolyte accumulation; maintain photosynthesis pigments and nutrient balance	Hussain et al. (2019)
Inbred line DT-287M and DS-753F	Seedling stage (roots)	Drought-tolerant-287M higher SOD and ascorbate peroxidase activity than drought-susceptible-753F	Zheng et al. (2020)
Maize Hybrid Naudi	Seedling to maturity	Moderate drought increase in leaf chlorophyll and carotenoid content and K/Na ratio	Leila Romdhane et al. (2019)
Eight Commercial cultivars	Two weeks after germination	Osmoprotectants like proline and GB can be used as stress tolerance indicator	Shafiq et al. (2019)

Abbreviations: *SOD* superoxide dismutase, *CAT* catalase, *GB* glycine betaine, *MDA* malondialdehyde, *APX* ascorbate peroxidase, *H2O2* hydrogen peroxide was observed in Dong Dan 80, and this was associated with higher photosynthetic activity, osmolyte accumulation, and antioxidant activities and lower lipid peroxidation as compared with Run Nong 35. Overall, the cultivar Dong Dan 80 was better able to resist the detrimental effects of progressive drought stress. Plants respond to drought stress through various physiological and biochemical changes. Exposure to drought leads to cellular dehydration; in response, plants increase the production of specific sets of primary and secondary metabolites that act as osmo-protectants and osmolytes (Ashraf and Akram 2009). These accumulated solutes lower the cellular osmotic potential and draw water into the cell to maintain turgor pressure. Moreover, osmo-protectants preserve the cellular apparatus from the damage caused by dehydration, without interfering with the normal metabolic processes at the cellular level (Van Oosten et al. 2017). Plants also produced several amines (polyamines and glycinebetaine), amino acids (proline), soluble sugars (glucose, sucrose, trehalose), and polyols (mannitol, sorbitol, and inositol) (Singh et al. 2015). An elite maize inbred line DH4866 was transformed with the *beta* gene from *Escherichia coli* encoding choline dehydrogenase (EC 1.1.99.1), a key enzyme in the biosynthesis of glycine betaine from choline. The transgenic maize plants accumulated higher levels of glycine betaine and were more tolerant to drought stress than wild-type plants (non-transgenic) at germination and the young seedling stage. Most importantly, the grain yield of transgenic plants was significantly higher than that of wild-type plants after drought treatment. The enhanced glycine betaine accumulation in transgenic maize provides greater protection of the integrity of the cell membrane and greater activity of enzymes compared with wild-type plants in conditions of drought stress (Quan et al. 2004). However, some crops have low levels of these compounds; to increase the level of the manipulation of genes involved in osmo-protectant biosynthesis pathways is one of the strategies to improve stress tolerance in plants (Reguera et al. 2012). Furthermore, the mechanism of plant acclimation to stress depends on the metabolic plasticity as well as biosynthesis and accumulation of osmo-protective compounds. A general increase in metabolite levels under drought stress was observed in maize plants, including changes in amino acids, sugars, sugar alcohols, and intermediates of the TCA cycle (Witt et al. 2012). The metabolic pattern of different maize tissues like leaf blade, leaf sheath, ear, husk, and silks showed most contrasting metabolic pattern due to drought stress treatment. Also among all tissues, the leaf blade displaying the most considerable metabolome changes due to water deficiency. The effect of drought stress on water relation has been manifested at cellular as well as whole plant level. Maize leaf provides an excellent experimental model for molecular studies of the developing tissues (Avramova et al. 2015). Tolerant maize hybrids experience a smaller impact of drought on cell division due to a smaller reduction of leaf meristem size and number of dividing cells. The leaf meristems of these hybrids are better protected during the stress, particularly due to a higher activity of the redox-regulating enzymes CAT, POX, APX, and GR, resulting in less H2O2 production in these zones, allowing improved growth under drought conditions (Avramova et al. 2017).

3.2 Priming Improves Biochemical Mechanism of Drought Tolerance

Seed priming is the control of hydration of seeds in water or a solution of low osmotic potential to initiate the germination metabolism without radical protrusion. Seed priming is known to trigger the normal metabolic developments during early stage of germination, before the radicle protrusion (Hussain et al. 2019). Presoaking maize grains with methyl jasmonate (MeJA) led to increases in total carbohydrates, total soluble sugar, polysaccharides, and free amino acids, proline, and total protein content. Moreover, the application of the investigated MeJA significantly improved growth hormone in terms of IAA. In contrast ABA level was markedly declined in maize plant. The activities of oxidative CAT, POX, and SOD were also increased with MeJA (Abdelgawad et al. 2014). Two maize (*Zea mays* L.) cultivars, that is, Shaandan 9 (S9) and Shaandan 911 (S911), were treated exogenous glycinebetaine (GB). The foliar application of GB increased the concentrations of all osmolytes measured, DM and GY of both cultivars under DS. These positive responses of exogenous GB spray were more pronounced in S911 as compared to those in S9 (Zhang et al. 2009). The combined pretreatments with exogenous MeJA+SA mitigated the adverse effects of drought-induced oxidative stress, as reflected in lower levels of lipid peroxidation, LOX activity, and H2O2. Exogenous applications of MeJA+SA approximately doubled the activities of the antioxidant enzymes catalase, peroxidase, and superoxide dismutase. The same pretreatment also maintained adequate water status of the plants under drought stress by increasing osmolytes including proline, total carbohydrate content, and total soluble sugars. The results show that seed and foliar pretreatments with exogenous MeJA and/or SA can have positive effects on the responses of maize seedlings to drought (Tayyab et al. 2020). Exogenous application of ascorbic acid in two maize cultivars Agaiti-2002 (tolerant) EV-1098 (sensitive) lowered the drought stress-induced reduction in growth, fresh and dry biomass, and photosynthetic pigments. Application of AsA further enhanced the activity superoxide dismutase (SOD) and peroxidase (POD) enzymes in maize plants. The results indicate that foliar application of AsA alleviated the detrimental effects of drought stress in the maize plants by improving the antioxidative defense system (Noman et al. 2015). In response to drought stress and to counteract reactive oxygen species, leaves and roots showed significant transcriptional upregulation of glutathione synthesis (GSH1) and reduction (GR). However, the growth of leaves arrested due to low flux of sulfur from sulfate into cysteine and glutathione of drought-stressed plants, ultimately resulting in enhanced oxidative stress, which together contribute to growth arrest of leaves. The low flux of sulfur into glutathione is a result of decreased SERAT activity and low sulfate availability. In contrast, roots accumulate sulfate to support sulfide, cysteine, and glutathione formation and maintain growth. The results evidence a significant and organ-specific impact of drought upon sulfate assimilation in the staple crop maize. We conclude that the antagonistic regulation of sulfur metabolism in leaves and roots enables a successful drought stress response at the whole plant level (Ahmad et al. 2016). Exogenous application of Spermidine (Spd) on two maize cultivars, Xianyu 335 (drought resistant) and Fenghe 1 (drought susceptible), reduces oxidative damage by enhancing the antioxidant components, raising the redox state of ascorbate and glutathione, and altering the polyamine pool; the improvement is much greater in Xianyu 335 (drought resistant) than Fenghe 1 (drought susceptible) (Li et al. 2018).

4 Role of Biotic Factors to Modify Physiological and Biochemical Process in Drought Tolerance

Water deficit foremost restricts the plant growth, development, and yield mainly in arid and semiarid regions causing economic loss in agriculture. Plant growth-promoting rhizobacteria are habituated in adverse environmental conditions; plants were often inoculated with beneficial microorganisms because they protect plants with drought and promote plant growth (Glick et al. 1997; Timmusk and Wagner 1999; Marulanda et al. 2007, 2008). Bacterial cells under drought stress build up compatible solutes like amino acids, quaternary amines, and sugars that stop deteriorating processes and enhance cell development in unfavorable osmotic conditions (Potts 1994). The PGPR-induced tolerance is termed as "induced systemic tolerance" (IST) (Yang et al. 2009). In a study, the effect of inoculated maize plants with genetically engineered *Azospirillum brasilense* strains that over-accumulate trehalose was analyzed. Eighty-five percent of maize plants inoculated with transformed *A. brasilense* survive drought tolerance through increase in leaf and root biomass and higher accumulation of trehalose compared to wild-type *A. brasilense* that did not accumulate significant levels of the disaccharide (Rodríguez-Salazar et al. 2009). Moreover, seed bacterization of maize with three EPS-producing bacterial strains (*Proteus penneri* (Pp1), *Pseudomonas aeruginosa* (Pa2), and *Alcaligenes faecalis* (AF3)) in combination with their respective EPS showed improved soil moisture contents, plant biomass, root and shoot length, and leaf area. Under drought stress, the inoculated plants showed increase in relative water content, protein, and sugar though the proline content and the activities of antioxidant enzymes were decreased (Naseem and Bano 2014). Similarly, maize seedlings inoculated with *Bacillus* spp. showed physiological response that could alleviate drought stress-negative effect on osmoregulation by increased proline, sugars, and free amino acids and decreased electrolyte leakage. Inoculation reduced the activity of antioxidant enzymes ascorbate peroxidase, catalase, and glutathione peroxidase (Vardharajula et al. 2011). During infertile or drought conditions, maize is an effective host for arbuscular mycorrhizae (AM) (Boomsma and Vyn 2008). So far few studies have been conducted to examine the morpho-physiological effects of AM infection on maize drought tolerance. The symbiotic relationship between AM and roots increases the productivity of various crops including maize (Sylvia et al. 1993). AM fungi often alter rates of water influx and efflux in host plants, thus affecting tissue water content and leaf physiology. Other impacts of AM symbiosis involve changes in stomatal conductance (gs) and transpiration (T), typically higher, while conductance (gs) unaffected or greater during drought stress in AM relative to non-AM plants (Augé 2001) also delays reductions in leaf water potential (Cw) during periods of drought stress. The role of biotic factors is listed in Table 2.

Table 2 Inoculation with beneficial microorganism and changes in physio-biochemical responses of maize crop under drought stress

Beneficial microorganism	Physiological biochemical changes	References
G. intraradices (arbuscular mycorrhizal AM)	Enhance leaf water potential and RWC and recover in less time after rewatering	Subramanian et al. (1997)
Pseudomonas spp.	Improved plant biomass, RWC, leaf ψ, soil/root tissue ratio, high proline, sugars and free amino acids, decreased electrolyte leakage, and low antioxidant enzyme activity	Sandhya et al. (2010)
Azospirillum lipoferum produced ABA and GA	Alleviate water stress effects on maize plants	
Azospirillum strain Az19 more tolerant than Az39	Osmotic stress tolerance	García et al. (2017)
Pseudomonas putida strain FBKV$_2$	Better growth in shoot, root length, and dry biomass. Also improved cellular metabolites and stomatal conductance	Vurukonda et al. (2016)
B. thuringiensis or AM fungi or combination of both	*Bt* increase accumulation of nutrients. *Combination of both* (*Bt + AM fungi)* reduced oxidative damage; *AM fungi* maintain homeostatic or improved tolerance	Armada et al. (2015)
Pseudomonas putida, *Pseudomonas* sp., and *Bacillus megaterium*	*P. putida* and *B. megaterium* increased osmotic stress tolerance, proline content, shoot and root biomass, and water content. *Pseudomonas* spp. decrease IAA production	Marulanda et al. (2009)
Azospirillum	Accumulates trehalose	Rodríguez-Salazar et al. (2009)
Bacterial endophytes-*Burkholderia Phytofirmans* strain PsJN and *Enterobacter* sp. FD17	Bacterial inoculation minimize the drought effects; increase in shoot/root biomass, leaf area, chlorophyll content, photosynthesis, and PSII efficiency	Naveed et al. (2013)
Azotobacter strains (PGPR) Az63, Az69, and Az70	Increase shoot dry weight; plant height; chlorophyll content; and N, P, and Fe concentrations	Shirinbayan et al. (2019)
Bacillus pumilus spp. + *L-tryptophan*	Increase RWC, osmotic potential, protein content, and photosynthetic pigments	Yasmin et al. (2021)
Azospirillum lipoferum strain	Accumulates more free amino acids and sugars. Also increase shoot/root fresh weight, dry weight, and length	Bano et al. (2013)
Arbuscular mycorrhizal fungi (AMF) and *PGPR*	Improves crop growth, yield, and drought tolerance	Zoppellari et al. (2014)
Arthrobacter arilaitensis and *Streptomyces pseudo venezuelae* (actinomycetes)	Protects deleterious effects of drought and increase in physiological parameters	Chukwuneme et al. (2020)
Bacillus spp. strains	Increases in dry biomass, plant height, and K+ and P+ uptake. Accumulates proline and modulates antioxidant system by decreasing ascorbate and glutathione reductase activity	Moreno-Galván et al. (2020)
P. putida strain FBKV2 transcriptomic analysis	Colonized roots; modulate metabolic, signaling, and stress-responsive genes	Ali et al. (2018)
Endophytic (PGPE) bacteria *Enterobacter cloacae* 2WC2 strain	Elevated the morphological variables, relative water content, and antioxidant activity	Maqbool et al. (2021)

5 Conclusions and Future Prospects

Water constrains reduced the plant growth, development, and productivity. Plants are sessile; they adapt through avoidance or developing resistance against the drought conditions. Maize plants' resistance mechanism involves the scavenging of ROS, free radicals, hydroxyl group, and H2O2 and thus maintains the metabolic homeostatic. Although priming has a significant effect on the drought-tolerant mechanism, the major shortcoming of this technique is due to different types of priming agents having different properties and effectiveness. Therefore, each plant species needs to be optimized for the priming solutions (Horii et al. 2007). Similarly, the potential benefits of biotic factors in drought tolerance are restricted to certain drought-prone, infertile regions of the tropics (i.e., portions of Africa and Asia) in which maize production does not commonly involve intensive irrigation and fertilizer application. Therefore, the long-term strategies include the development of drought-tolerant crop varieties. Maize is the staple food crop over the world's most regions, since long CIMMYT has been engaged to produce climate-resilient maize germplasm for increased tolerance to traits associated with a variable and changing climate, along with yield potential, defensive traits, and consumer-preferred traits. Further, to increase genetic gain and enhance the breeding progress for stress-prone environment, effective integration of modern tools and techniques is required like high throughput and precision, phenotyping, DH technology, and molecular marker-assisted breeding. Another way to develop drought-tolerant crops is through biotechnological approach; recently, many genes that are related to plant response to various abiotic stresses have been identified and described. To develop the drought-tolerant crop through genetic engineering, manipulation of single gene that affects the specific target can be employed. Overexpression of genes is associated with the accumulation of osmolytes, proteins, and enzymes of antioxidant system; ion transporters can be utilized to develop the novel drought resistance genotype. Therefore, selection of the drought-tolerant germplasm based on the physio-biochemical based may be helpful to develop the drought tolerance varieties.

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