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# Endophytic and rhizobacteria functionalities in alleviating drought stress in maize plants

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**Abstract:** Drought stress is among the significant forms of abiotic stresses that unfavourably affects maize survival as well as the development from germination to maturity. This paper, therefore, reviewed drought stress effects in maize plants and expatiated on the plausible adoptable mitigation measures to employ in curbing these effects as well. Water shortage prompts drought stress that alters the morphological, physiological and biochemical activities in maize plants. The major drought stress implications on the plant's survival are mostly in the area of altered metabolic functions, including nutrient metabolism, cell membrane integrity, water relationships, plant yield, photosynthetic processes, osmotic adjustment, and the pigment content. Mitigating strategies, such as the breeding of drought-tolerant varieties, genomic applications for drought tolerance enhancement in maize plants, as well as the use of rhizobacteria and endophytic bacteria, can be employed in alleviating drought stress and ensuring optimal maize productivity.

**Keywords:** crop improvement; crop yields; climate change; endophytic microbes; food security; sustainable agriculture

The consequences of climate change, especially alterations in weather patterns, are sternly affecting the agricultural productivity and food security on both global and regional scales. Climate change continues to be one of the greatest and most significant environmental challenges facing the world today (Fadiji et al. 2022). Even with the economies of most developing countries being based on agriculture, crop plant production continues to be on the decline due to the impact of abiotic stresses that include salinity, heat stress, drought, and other climatic factors (Jahan et al. 2019). Drought is a condition of extreme stress in which the desired precipitation level is not attained, affecting the hydrological cycle, thus causing a negative impact on the environment, economy, and society at large (Kumar & Verma 2018). Drought exists as multidimensional stress occurring principally as a result of the decline in rainfall, with accompanying dry spells (Harrison et al. 2021). Drought or water stress negatively impacts the plant growth and productivity and results in a significant concern in achieving the worldwide demand for food crops (Igiehon & Babalola 2021). Characterised by the closure of the stomata and a reduction in the cell growth, a depleted leaf water potential and turgour loss, a decrease in the water content, drought stress poses a serious risk to the yield and quality of plants, including maize crops (Cheng et al. 2018).

Maize (*Zea mays* L.) is a forage and food crop that is of great significance, serving as an essential raw material for the food industry and plays vital roles in ag-

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ricultural production and global economies (Zheng et al. 2020). Maize is a cereal crop that has high water demand requirements to complete its different life cycle stages, but with the mounting inclination with the ongoing climate change, a decrease in the maize quality and an increase in yield losses may occur as a result of the varying biotic and abiotic stresses (Pokhrel 2021). The maize crop is reported to be prone to drought stress, which adversely impacts the biomass production as well as the vegetative growth, not excluding the development of the yield parameters and reproductive organs (Badr et al. 2020). Consequently, it is pertinent to fully understand the knowledge of drought stress in maize crops to determine the best suitable mitigation strategies to ensure optimal productivity. This paper, therefore, provides a short overview of drought stress implications on maize plants and expatiates on the plausible adoptable mitigation measures including the role of rhizobacteria and endophytic bacteria in curbing these effects.

**Concept of drought stress from different perspectives and evaluation methods.** Plant species including maize are sessile organisms that are mostly exposed to abiotic stresses, particularly during their various life cycles (Umair Hassan et al. 2020). Their survival is primarily dependent on their strategic response attributes to be able to cope with the ever dynamic and stressful conditions (Jacques et al. 2021). Abiotic stresses mostly come from undesirable ecological conditions that hinder the functional diversity of microbes in addition to the soil's physicochemical properties, leading to substantial yield loss (Goswami & Suresh 2020). They are major limitations to the global food security and crop yields, and thus necessitate an instantaneous response. Among these abiotic or environmental stresses, drought is among the most significant ones that limits the plant performance as well as survival, affecting the plant functions, including morphological, biochemical, metabolic, and physiological changes (Hera et al. 2018). From an agricultural context, a drought is a prolonged period of deficient precipitation or lack of momentous rainfall which restricts the water accessibility and results in negative impacts on the crop growth or yield (Abid et al. 2018). It is also seen as an inexorable factor that subsists in different milieus without taking cognizance of boundaries with no clear awareness (Seleiman et al. 2021). Plants' capability to maintain physio-biochemical functions during drought conditions and recuperate rapidly once the stress is curtailed is inviolable to ensuring sustainable crop plant production under recurrent drought events. This is necessary as plant growth and productivity depend on various cell processes, which are impacted by drought stress due to a decline in the energy supply for photosynthesis, enzymatic activities as well as cell division, elongation, and differentiation (Zhang et al. 2019). Drought creates grave and sweeping implications on the agricultural productivity. Since it is typified by occurring in severe arid climates and places with inadequate water resources, it has been reported to have a remarkable impingement on crop productivity (Wan et al. 2022). Drought stress is becoming more frequent due to the obvious unpredictable distribution of the rainfall and changes in climatic patterns, lowers the survival rate of seedlings, and increases a post-pollination embryo's likelihood of being terminated, ultimately leading to a reduced yield. Drought in maize crops can be monitored using two different methods. The first one appraises agricultural drought by utilising ground observational data (like soil, vegetation, and meteorology), comprising precipitation, temperature surveillance, soil moisture, and cropland vegetation indices (Li et al. 2019; Hunter et al. 2021). A wide range of evaluation systems to analyse the drought status are based on pedologic (Uwizeyimana et al. 2019) or meteorological (Mpandeli et al. 2019) indicators along with the crop's development and growth characteristics (Moon et al. 2020). Notably, the aforementioned indicators are limited in their spatial representation because they are on the point scale. Although this method can provide exact facts regarding agricultural-related drought parameters, it is reported to have limitations regarding any temporal and spatial discontinuity, aside from the high cost of research connected to it (Wan et al. 2022). The second method type, which include remote sensing techniques, possesses the edge of spatially low-cost monitoring. This method has turned out to be the predominant method of drought evaluation research (Wei et al. 2020). According to Wan et al. (2022), the main tenet behind this method is to access the drought or spectral indices, which echo the plant drought. This method is labour-saving and has a wide monitoring space range and time, while possessing the edge for temporal and spatial continuity. Advances in remote sensing technologies transformed drought monitoring by facilitating the unceasing observa-

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tions of vital drought-related variables over large spatial and temporal scales (Wang et al. 2020). With the use of this method, the degree of crop drought can be estimated based on the correspondence of remote sensing indices with the growth as well as the development of indicators that include the canopy temperature, soil moisture content, and crop phenotypic characteristics (Yang et al. 2017). Generally, the accuracy of any evaluation method is often particularly improved when the meteorological parameters, as well as the spectral indices, are jointly used. For instance, the temperature–vegetation drought index (TVDI), which is based on the premise of a simplified triangle space of the land surface temperature-normalised difference vegetation index (LST-NDVI), is a valid pointer to crop drought (Wei et al. 2020; Wan et al. 2021). A comparison of ground observation and remote sensing methods is summarised in Table 1.

**Drivers of drought stress in maize: Major causal factors.** Maize is a strategic and essential grain crop cultivated in different agro-ecological precincts globally (Mushayi et al. 2020). It is a crop that ably makes use of sunlight and moisture to produce a bountiful yield. Although maize is a warm-season crop, that is subtly sensitive to high-temperature stress, as such, drought stress is a serious pitfall to the global maize crop productivity (Tesfaye et al. 2018). Having been considered the key environmental stress for a variety of plant species including maize, drought has been documented as the most single critical threat to global food security (Okorie et al. 2019; Diatta et al. 2020). The main driver for drought stress in most plants including maize is reportedly known to be a deficiency in a water input from rainfall, though the loss of soil water via evaporation (as a result of high temperatures), dry wind, and a high light intensity have also been implicated (Cohen et al. 2021). Some causal factors have also been indicted as being responsible for drought stress and are mostly due to variations in the climatic patterns. For instance, the contribution of global warming due to the increase in the environmental temperature is not only leading to water losses or shortages in soils, but likewise in crop plants not excluding maize fields (Seleiman et al. 2021). The available internal plant water is lost to a great extent due to the heightened temperatures elicited from the climatic change that is already causing water deficit issues within the global agricultural system (Pepe et al. 2022). Similarly, detrimental changes in rainfall distribution patterns and intensity continue to exacerbate drought stress conditions; especially, in areas where crop plant production largely depends on the availability of rainfall (Konapala et al. 2020). This is a result of prominent anthropogenic activities like urbanization, industrialization as well as deforestation which have affected the water availability to maize plants through their impacts on the rainfall patterns, particularly via their influence on the climate change (Rather et al. 2022).

**Drought stress in maize plants: Implications and effects.** The maize or corn plant is a significant food, feed and biofuel crop that makes a considerable contribution to ensuring food availability, livestock production (being an essential dietary component in animal feed formulation) and to the energy sector (Bodhankar et al. 2020). However, the production output of maize is not sufficient enough

Table 1. A comparison of the two monitoring methods of drought in maize crops

| S/N | Ground observation method | Remote sensing method |
|---|---|---|
| 1. | High cost of research is involved | It is cost-effective and labour-saving |
| 2. | Performance is based meteorological or pedologic indicators | Performance is independent of the meteorological and field survey data |
| 3. | Has limitations as regards to temporal and spatial discontinuity | Has the advantage of spatial continuity |
| 4. | Monitoring accuracy is often limited in regions with sparse observation stations distributions | Allows for continuous monitoring due to multi-temporal and high-resolution spatial coverage |
| 5. | Interpolation of data points may be affected due to loss of historical data records | Data records are readily accessible and do not affect the interpolation of data points |
| 6. | Observations data may not be sufficient to capture the spatio-temporal variability of drought-related variables like precipitation | Spatio-temporal acquisition of near real-time data are sufficient |
| 7. | Consistent global drought analysis may be quite challenging | Possess the capability for consistent global drought analysis |

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to meet with the utilisation demand. For instance, the demand for maize in sub-Saharan Africa is anticipated to increase by 30% by the year 2050 considering increasing population growth (Ekpa et al. 2018). Therefore, optimal maize production must be boosted to ensure food security and has become an urgent need (Zhang et al. 2021), though not without some limiting factors. One of the factors affecting maize productivity is a drought (Chukwuneme et al. 2020a) with a reported average annual yield loss calculated to be about 15% of the global potential yield (Adewale et al. 2018). The implications and effects of drought stress on maize production are overwhelming as it is an important staple cereal food and a cultigen of global economic importance (Kennett et al. 2020).

Drought stress is the main driver of losses for maize production and it has caused active deviations in the plants' physio-biochemical functions including respiration, photosynthesis, transpiration, enzyme activity, and hormonal metabolism (Webber et al. 2018; Kaur & Kumar 2020). Plants including maize put forth wide-ranging sequences of reactions to drought stress conditions, which are seen in an array of adjustments in their biochemical and morpho-physiological parameters. On the plant morphological characteristics, drought stress has been reported to cause a decrease in the yield and growth, as well as reducing the seed germination capability (Khan et al. 2018; Danish et al. 2020a). This decrease in yield or growth retardation could be a result of excessive evaporation, disruption of the photosynthetic machinery, the decline in carbon acclimatisation as well as inhibition of the cell expansion (Sharif et al. 2018; Bogati & Walczak 2022). Drought exposure during the seedling stage has been reported to induce a substantial reduction in the overall maize biomass, thereby altering its phenotypic attributes and subsequent yield (Saad-Allah et al. 2021). Song and Jin (2020) equally documented how drought stress caused maize anthesis, a prolonged growth stage, and a delay in maturity dates during the seedling stage. Drought stress also elongates the vegetative growth period as well as shortens the reproductive stage's growth period (Bhusal et al. 2021). It affects the vegetative stage of the maize plant, restricting the function and structure of the leaf, stem, and root while the reproductive stage inhibits the silk and tassel development (Pokhrel 2021). Also, the plant height is usually reduced in drought conditions and this is mainly a result of the reduced cell expansion, impaired mitosis, higher leaf senescence, accelerated leaf shedding, and other associated plant internal mechanisms to boost the plant height (Abreha et al. 2022). Likewise, a reduction in the number of flowers as well as the dry and fresh biomass decreased the nodulation and nodule functioning, as well as causing a high root-shoot length, have all been reported as consequent implications of drought stress (Wilmowicz et al. 2020; Hanaka et al. 2021).

Furthermore, an easily observed characteristic of a drought-stressed crop plant is the leaf area modification, which is often significantly reduced in many plant species including maize though its increase is majorly dependent on the turgour pressure of the leaf, availability of photo-assimilates, and canopy temperature (Kannenberg et al. 2018). Hussain et al. (2019) also examined the effect of drought stress on maize hybrids and reported a notable decrease in the plant height, shoot dry and fresh weights, in addition to the leaf area. On the maize crop's physiology and biochemistry, the decreased relative water content is often the initial consequence of drought stress in most plants including maize. A decreased relative water content usually reflects in a substantial reduction in the leaf water potential which may result in stomata closure (Umair Hassan et al. 2020). A decreased relative water content in maize often results in an elevated leaf temperature due to a decrease in the transpiration cooling (Bhusal et al. 2021). One parameter often used as a pointer to the presence of photosynthetic damage in plants is the quantification of the chlorophyll fluorescence (Toscano et al. 2019).

Bhusal et al. (2021) reported a reduced chlorophyll content as well as gas exchange attributes in maize while Aslam et al. (2021) chronicled a decline in the chlorophyll content in their study and ascribed the loss to certain deleterious impacts on the photosynthetic apparatus due to drought stress. Drought stress considerably reduces the chlorophyll content and pigment composition as a result of the heightened oxidative stress or chlorophyll pigments' photo-oxidation (Hussain et al. 2019). Drought stress conditions often lead to the synthesis of reactive oxygen species (ROS) (Hewedy et al. 2020). Zheng et al. (2020) indicated that drought stress conditions lead to the accumulation of ROS in maize cells. ROS are the unfavoured products of the biochemical alterations that a plant's expo-

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sure to drought stress generates (Khayatnezhad & Gholamin 2021). In order to scavenge the high levels of ROS eliciting from the drought stress, plants including maize crops have devised both complex enzymatic and non-enzymatic structures. The non-enzymatic complex involves reduced vitamin E, glutathione, ascorbic acid, flavonoids, mannitol, as well as carotenoids while the enzymatic system involves the production of glutathione peroxidase, glutathione reductase, catalase, ascorbate peroxidase and superoxide dismutase (SOD) (Seleiman et al. 2021; Yang et al. 2021). The generation of ROS often results in the degeneration of the structural and functional proteins, membrane damage, enzyme inactivation, oxidative damage, as well as peroxidation of the lipids (Gao et al. 2020; Dubey et al. 2021). When the photosynthetic activity is decreased and light excitation energy is surplus to requirements, the photosynthetic pigments' hyper-excitation in the plant antenna may ensue, resulting in the ROS accumulation in the chloroplasts (Toscano et al. 2019). In photosynthesis, the reduction in photosynthetic activities can be seen as the major effect of drought stress due to the increased leaf temperature, reduced leaf expansion, stomatal closure, and impaired photosynthetic machinery (Huan et al. 2020). Photosynthesis is the major driver for crop productivity and the reduction in the photosynthetic activities in drought stress conditions is due to the non-stomatal and stomatal restrictions. The non-stomatal restriction occurs during severe drought conditions, while the stomatal restriction majorly influences the decrease in the photosynthetic performance particularly in mild drought conditions (Bogati & Walczak 2022) such that when the extent of drought is mild, the stomatal conductance reduces due to the decreased leaf water potential, and the environmental absorption rate of $CO_2$ drops, resulting in a reduced rate of photosynthesis in the leaves (Xu et al. 2022). Summarily, as depicted in Figure 1, the biochemical and physiological response mechanism to drought stress results from a complex pathway of responses, beginning with the level of stress, which sets off a chain of molecular mechanisms and concluding at different levels of physiological, metabolic, molecular, and developmental responses (Sharma et al. 2022).

Molecularly, drought stress creates modifications in how the transcription factors are expressed and have been connected to the productivity of maize (Zheng et al. 2020). The molecular backwash of drought stress in plants is often seen on the gene expressions and has been reported to induce fluctuations in the patterns of gene expression, as well as changes in the manifestation of molecular chaperones and late embryogenesis abundant (LEA)/dehydrin genes whose responsibility is to prevent cell protein denaturation (Hussain et al. 2018). Furthermore, the molecular processes that are responsive to drought stress include water channel proteins, stress-responsive proteins, transcription factors, and signalling pathways. By protecting the cellular contents or controlling the stress-responsive genes, these chemicals help to provide drought resistance. (Razi & Muneer 2021). Transcription factors are

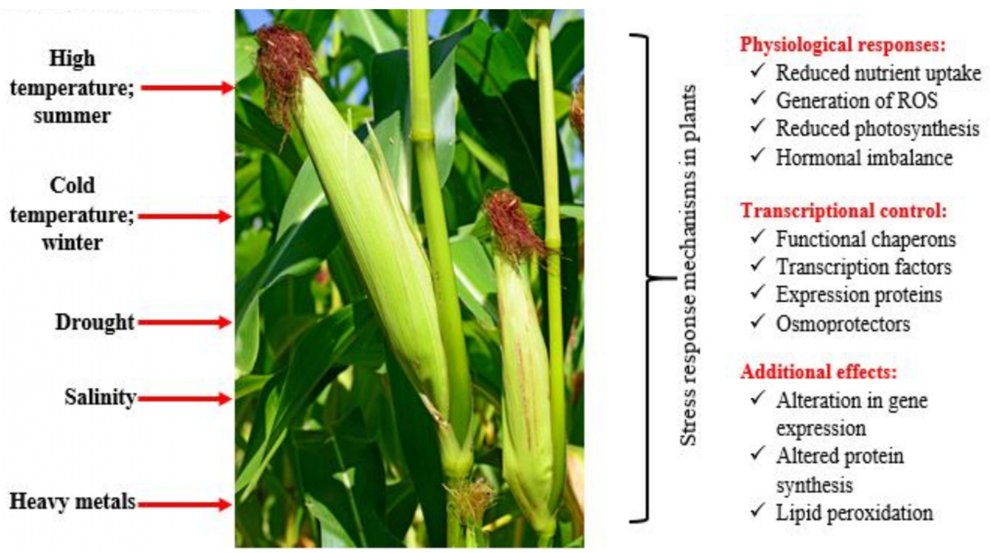


Figure 1. The maize plant response to drought stress

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the natural master regulators of cellular functions that also modify the characteristics in response to stress. (Giannopoulou et al. 2022). Due to the complicated tolerance mechanism, single gene engineering that encodes for a specific protein is insufficient to establish a tolerance (Olechowska et al. 2022). Myeloblastosis-related proteins, NAC (no apical meristem, Arabidopsis 58. transcription activator factor, and cup shaped cotyledon), and basic helix-loop-helix are transcription factors that interact with the cis-regulatory regions to activate gene transcription and translation, allowing for adaptation to water deficiencies (Liu et al. 2021). A critical step in the development of drought-tolerant cultivars is the discovery of specific genes and pathways associated with drought tolerance (Davoudi et al. 2022). With the use of transcriptome sequencing, it is now possible to characterise molecular regulators in-depth and look at the genes that are involved in the response to drought (Pazhamala et al. 2021).

In response to drought stress, maize develops differentially expressed genes, primarily transcription factors, hormonal signalling, stress defence, detoxification, and genes related to photosynthesis. These differentially expressed genes are useful for elucidating the molecular mechanisms by which maize responds to drought (Liu et al. 2021). Waititu et al. (2021) emphasised that plant genotypes have a significant impact on the molecular responses to stress. Unfortunately, more thorough research on the transcriptional alterations caused by drought stress in maize plants is still lacking. In addition, two of the abscisic acid (ABA)'s primary distinctive activities include controlling the plant water balance and tolerating the osmotic stress (Jan et al. 2021). Numerous crops, including maize, have produced ABA mutants, which are unable to thrive when exposed to temperature and drought conditions. Short-stemmed plants are produced by ABA mutants, demonstrating the role of ABA in controlling the cell cycle and other cellular processes. Recent developments in molecular biology have shed light on the molecular mechanisms underlying the increased accumulation of ABA in response to osmotic stress, and the accumulation of ABA depends on the equilibrium of the ABA production and degradation (Zhang et al. 2022a). Aslam et al. (2021) reported that numerous ABA biosynthesising genes like ZEP, 9-cis-epoxycarotenoid dioxygenase, ABA aldehyde oxidase, and LOS5/ABA3 are up-regulated in response to drought stress.

The up-regulation of ABA-dependent genes starts following an increase in the ABA production in response to drought stress. Aquaporins, osmolyte, LEA, dehydrins, chaperones, detoxifying enzymes, ubiquitination-associated enzymes, and proteases are examples of genes up-regulated in the osmotic homeostasis (Arif et al. 2021).

For instance, aquaporins (AQPs), which are found in crop plants like maize, are recognised to be crucial in maintaining water homeostasis. The short-term alterations in the root hydraulics and leaf water relationships are mediated through AQPs, according to numerous physiological and genetic research studies (Kapilan et al. 2018). In times of dryness, the movement of water within and across the cells is determined by the controlled activity and abundance of the AQPs (Shekoofa & Sinclair 2018; Kurowska et al. 2019). An aquaporin gene expression study has been performed on crops under drought stress (Shivaraj et al. 2021).

**Adoptable strategies to mitigate the devastating effect of drought stress on maize plants.** The intermittent re-emergence of drought stress makes it imperative to develop procedures that may be utilised to cushion its effects (Abid et al. 2018). Most times, drought conditions are complemented with detrimental effects like pathogenic attack, heat, and salinity. Hence, plants undergo various morphological and physiological modifications that are not limited to osmotic adjustments, a reduced transpiration and photosynthesis rate, modified stress signaling pathways, overproduction of reactive oxygen species, senescence, as well as repressed shoot and root growth (Ahluwalia et al. 2021).

To enhance maize crop production under conditions of drought stress, there is a need for the basic comprehension of the attributes or traits sustaining the plant performance with strategies that ensure the maximal productivity (Jochum et al. 2019; Condon 2020). Many of the adoptable strategies can be run concurrently when maize plants undergo drought stress as many of them can be employed (singly or in combination) to ensure optimal productivity under unfavourable drought conditions (Delfin et al. 2021). Firstly, the use of efficient and sustainable planting methods and techniques can be used. Various methods and techniques of planting are now being used in maize crop production; especially, to conserve water and increase its use efficiency. Good planting practices, contouring, mulching, and the use of effective irrigation meth-

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ods are believed to also aid or enhance the tolerance to drought stress (Solis et al. 2018). Gamma-polyglutamic acid, which can be employed as a soil conditioner and water-retentive agent to increase the agricultural productivity, has also been discovered in recent studies to play a significant role in plant growth and regulation. As a result of its excellent water solubility and retention, biodegradability, and harmlessness, it has drawn more attention as an environmentally friendly fertiliser synergist (Guo et al. 2017; Liang & Shi 2021). It is a D/L-glutamic acid monomer-based biopolymer that is fermented by *Bacillus subtilis*. It is non-toxic, water-soluble, biodegradable, and environmentally beneficial (Wang et al. 2022). It has been reported that exogenous administration of γ-PGA could considerably improve the plants' ability to withstand stress (Xu et al. 2020). Most of the earlier research on crops, like the cucumber and *Brassica napus*, concentrated on the effects of cold and salt stress. For instance, it was discovered that γ-PGA may improve *Brassica napus*' tolerance to salt and cold by triggering the crosstalk between $H_2O_2$ and $Ca^{2+}$ signals and might improve its resilience to drought by encouraging ABA accumulation. Gamma-polyglutamic acid has not received much attention as a means of reducing drought stress in maize plants. However, very little research has examined the impact of γ-PGA on the plants' ability to withstand drought, particularly crops (Ma et al. 2020).

The regulatory mechanism of γ-PGA in the drought resistance of maize remains unclear (Batool et al. 2022). To comprehend the mechanism by which the exogenous application of γ-PGA to alter the drought resistance of maize, it is possible to study the changes in the rhizospheric and endophytic microbial population after and during the exogenous application of γ-PGA.

Secondly, the breeding of drought-tolerant or drought-resistant varieties is another method that can be used. This involves plant breeding techniques which utilise procedures of cultivating better wild-type species of maize plants that can withstand harsh drought conditions (Chandra et al. 2021). The application of this method in maize plant production will ensure that the potential of a high plant yield as well as improving the crop for drought tolerance are harnessed, which is the major focus of breeding programmes as it is critical to guarantee the stabilised global maize production (Rida et al. 2021). Breeding for stress tolerance requires careful consideration of the selection technique to be used. Selecting for the yield in unstressed conditions and then evaluating those choices at numerous sites with varying moisture availability, or "random stress", is perhaps the most popular technique (Riache et al. 2021). The underlying presumptions of the approach are that genes for drought tolerance are present in elite high-yielding material, even after the number of genotypes has been reduced to the few that were evaluated under random stress, and that selections under ideal growing conditions can also improve the performance under less than ideal circumstances (Khadka et al. 2020). Furthermore, hybrids typically produce more under drought than varieties with heterosis serving as a significant source of stress resistance (Sah et al. 2020). The genetic approach that improves drought tolerance in many plant species, such as maize, has been recently hypothesised (Zia et al. 2021). Genes linked with the SOD enzyme production can be incorporated into the maize crops to produce drought-tolerant transgenic varieties. Also, the application of transgenic or genome editing approaches assists in introducing preferred drought stress-resistant traits (Dubey et al. 2021). In a similar vein, genomics provides previously unheard-of opportunities for breaking down quantitative traits into their genetic components, the so-called quantitative trait loci (QTL), opening the door to marker-assisted selection and, eventually, the cloning of QTLs and their direct manipulation through genetic engineering (Sarma et al. 2021). In general, genome editing approaches will open up new possibilities for nucleotide-specific alterations and may be used in the future to increase the plants' resistance to drought. As a result, they are expected to become a common strategy for maintaining the global food security (Dubey et al. 2021).

Consequently, it is possible to locate significant QTLs controlling certain drought responses, which will offer an effective method of increasing drought resistance in the maize germplasm (Nepolean et al. 2018).

There is disagreement among many researchers over the ideal route to take when breeding maize to withstand droughts, and others suggest combining two or more of the aforementioned methods (Kamal et al. 2021). Lastly, the use of osmoprotectants and growth regulators periodically has shown an encouraging impact on tolerance to drought stress (Chandra et al. 2021). Applying these com-

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pounds has improved plant characteristics like the morphology, relative water content, photosynthetic capacity, as well as gas exchange capabilities (Huan et al. 2020). They are majorly classified into hormones (like abscisic acid, salicylic acid, melatonin), nutrients (like nitrogen, phosphorus, potassium), polyamines (such as spermidine, putrescine, spermine), sugars (like trehalose, chitosan) amino acids (like proline, lornithine, arginine), and others (like the α-lipoic acid) as documented by Aslam et al. (2021). Considerable quantities of osmoregulatory agents, such as proline, free amino acids as well as glycine betaine (GB), have been reported to be accumulated by the maize plant during drought conditions (Saad-Allah et al. 2021). For instance, the application of proline on leaves promotes the internal free proline content which boosts the crop's antioxidant defence system and photosynthetic performance (Semida et al. 2020). Likewise, the application of polyamines is also effective and has been documented for enhancing plants' drought stress tolerance, especially in barley, wheat, and maize (Sallam et al. 2019). Classification of osmoprotectants and growth regulators is visualised in Figure 2.

**Alleviating drought stress in maize plants: Role of rhizobacteria and endophytic bacteria.** Drought has been noted to be a key factor that affects the yield of maize and, as such, whatever strategy to address it will be of immense benefit (Siddique et al. 2022). While most crops are susceptible to drought conditions and may experience losses in yield of more than 50%, maize has been reported to be more sensitive to drought than other grains (Rida et al. 2021). In fact, the occurrence of drought stress conditions especially at the vegetative and reproductive phases of maize reduces yields by 39.3% (Lunduka et al. 2019).

The role of rhizospheric microbes in maize plants as bioinoculants in mitigating drought stress is summarised in Table 2 while that of endophytic microbes is exemplified in Table 3.

Maize responds to drought stress conditions through a sequence of biochemical, molecular, physiological, and morphological changes (Chukwuneme et al. 2020a). Most times, the responses are inclined by associations between the hosts and the allied endophytic and rhizosphere microbes (Bodhankar et al. 2020), which has attracted research interest in recent decades (Igiehon et al. 2019). Though adaptable strategies to allay the devastating impacts of drought stress in maize crops as discussed above may be costly and time-consuming (Niu et al. 2018), the use of microbial resources provides an emerging, safe, revolutionary, and sustainable remedy to the consequences of drought as the potential of rhizosphere and endophytic microbes in improving drought stress tolerance in plants to attain optimal productivity and sustainable agriculture has been expressly docu-


Figure 2. Classification of the osmoprotectants and growth regulators

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Table 2. Role of rhizospheric microbes as bioinoculants in mitigating drought stress in maize (*Zea may* L.)

| S/N | Country | Study performed | Rhizosperic microbes | Outcome | Reference |
|---|---|---|---|---|---|
| 1. | Multan, Pakistan | Drought-tolerant ACC deaminase including PGPR inoculated into maize under axenic conditions to reduce drought stress. | *Leclercia adecarboxylata* | *Leclercia adecarboxylata* was discovered to be a novel drought-tolerant ACC deaminase-containing PGPR that has the potential to ameliorate drought stress by enhancing root elongation, NPK absorption, and perhaps lowering ethylene levels in plants. | (Danish et al. 2020b) |
| 2. | Punjab, Pakistan | Drought stress alleviation in maize with and without timber waste biochar by ACC deaminase producing *Achromobacter xylosoxidans* and *Enterobacter cloacae* (*Zea mays* L.) | *Achromobacter xylosoxidans* and *Enterobacter cloacae* | Due to the potential for increased (ACC)-deaminase synthesis, improved nutrient solubilisation, and (IAA) production, *Enterobacter cloacae* is more effective than *Achromobacter xylosoxidans* in increasing maize yield under drought stress, with 15 Mg/ha timber waste biochar. | (Danish et al. 2020a) |
| 3. | Alabama, USA | Drought stress and the effect of plant growth-promoting rhizobacteria on maize growth | | The findings show that PGPR inoculation can promote improved plant root development (through the synthesis of plant growth regulators), resulting in greater water and nutrient absorption from the soil. | (Lin et al. 2020) |
| 4. | Punjab, Pakistan | Inoculation of *Bacillus* spp. strains under sterile soil conditions ameliorates drought stress in maize (*Zea mays* L.). | *Bacillus* spp. | The differences in the examined biochemical characteristics, lipid peroxidation, and antioxidant responses show that stress alleviation is dependent on the unique plant–strain interaction. For sustainable agriculture, such bacteria could be employed to boost crop output and protect plants from biotic and abiotic challenges. | (Azeem et al. 2022) |
| 5. | Karaj, Iran | Under water stress, the physiological and biochemical responses of maize (*Zea mays* L.) seeded directly and transplanted with PGPR. | *Pseudomonas putida* | The study shows that transplanting method with plants treated with Pseudomonas were found to be effective in reducing the negative effects of water stress on maize physiological and biochemical characteristics. | (Rezazadeh et al. 2019) |
| 6. | Massachusetts, USA | Cerium oxide nanoparticles applied to the leaves boost maize production under salt stress: homeostasis of reactive oxygen species and rhizobacteria regulation. | | $CeO_2$ NanoMaterials boosted the quantity of halotolerant plant growth-promoting rhizobacteria and increased the richness and diversity of rhizobacteria by increasing the carbon supply in root exudates (HT-PGPR). These findings will provide new insight into the usage of $CeO_2$ NMs in crop management to prevent salinity-related crop loss. | (Liu et al. 2022) |
| 7. | Kafr El-Sheikh, Egypt | Using plant growth-promoting rhizobacteria and silica nanoparticles to reduce the negative effects of water deficiency and soil salinity on maize growth and production. | *Azospir illum lipoferum* and *Bacillus circulance* | The use of silica nanoparticles in combination with PGPR has been shown to improve yield-related characteristics, maize productivity, and nutrient uptake (N, P, and K). As a result, combining them is a viable method for reducing the negative effects of water scarcity and soil salinity on maize productivity. | (Hafez et al. 2021) |
| 8. | South Korea | Rhizobacteria that promote plant growth and silicon *Pseudomonas psychrotolerans* CS51 protects *Zea mays* L. from salt stress. | *Pseudomonas psychrotolerans* | Finally, the current findings show that combining CS51 with silicon can be used to protect maize plants from salinity stress and could be commercialised as a bio-fertiliser. | (Kubi et al. 2021) |

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Table 2 to be continued

| S/N | Country | Study performed | Rhizosperic microbes | Outcome | Reference |
|---|---|---|---|---|---|
| 9. | Bahawalpur, Pakistan | Examining the potential of EPS-producing rhizobacteria with ACC-deaminase activity to improve maize growth and physiology in drought. | *Bacillus velezensis* | The strains having both ACC-deaminase and EPS-producing activity were found to be better suitable for boosting crop growth and physiology under drought stress. | (Nadeem et al. 2021) |
| 10. | Cotonou, Benin | Plant growth-promoting rhizobacteria in conjunction with chitosan on maize crops: intriguing potential for sustainable, environmentally friendly agriculture and abiotic stress resistance. | *Pseudomonas putida* | This study demonstrates how chitosan and rhizobacteria can be used as biostimulants to boost maize yield and productivity over time. | (Agbodjato et al. 2021) |
| 11. | South Carolina, USA | Drought resistance in maize (*Zea mays* L.) is conferred by cross inoculation of rhizobiome from a congeneric ruderal plant via changes in root shape and proteome. | *Andropogon virginicus* | The research shows a new way to use plant-rhizobiome relationships to improve drought tolerance in crops by providing a mechanistic explanation of how the rhizobiome facilitates drought tolerance. | (Zhang et al. 2022b) |

ACC – 1-aminocyclopropane-1-carboxylic acid; EPS – exopolysaccharides; IAA – indole acetic acid; PGPR – plant growth-promoting rhizobacteria

mented (Igiehon & Babalola 2018; Enebe & Babalola 2019; Thakur et al. 2021; Siddique et al. 2022). Plant growth-promoting rhizobacteria (PGPR) could stimulate the drought tolerance in crop plants including maize as some peculiar strains can transfer this ability to plants. Kushwaha et al. (2020) reported that the PGPR can also exist as endophytes in different plant parts and can positively stimulate growth during drought stress conditions. Endophytes are microorganisms that colonise the internal tissue of a plant, irrespective of being detrimental, beneficial, or neutral to their hosts. They are often seen to have a significant influence on the plant's physiological reactions due to their close immediacy with the host plant (Bodhankar et al. 2020). Though endophytic and rhizobacteria bacteria exist in varying ecological niches, their utilisation of comparable mechanisms to stimulate plant growth is noteworthy (Sood et al. 2020). They cause maize plants to survive drought stress to attain sustainable productivity by lessening the ethylene concentrations (Dhayalan & Sudalaimuthu 2021). The unique characteristics of these microbes are enshrined in their mechanistic ability to produce siderophores to quench iron, plant growth regulators (phytohormones), 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, nutrients as well as minerals like manganese, copper, zinc, and fix nitrogen (Uzoh & Babalola 2020). The ACC strain is the precursor of the ethylene (Danish et al. 2020a), while the PGPR strains include *Bacillus* spp. and *Pseudomonas* spp. produce ACC deaminase that catabolises ACC to α-ketobutyrate and ammonia, and protects the maize plant from the deleterious effects of drought stress (Kumar et al. 2019; Getahun et al. 2020). Generally, most PGPR stains curtail the deleterious impacts of stresses by increasing the amino acid content and Pro production, reducing the hydrogen peroxide content, in addition to increasing the total phenolics, synthesis of exopolysaccharides, as well as enhancing enzyme activities in most plants including maize. Therefore, the utilisation of PGPR as a mitigating stratagem in combating drought stress is proving to be of immense preference in attaining sustainable agriculture (Enebe & Babalola 2019; Ojuederie et al. 2019). Hence, PGPR can help plants to adjust to the adverse drought conditions and can ease drought stress by varying responses in the genomic field (Igiehon et al. 2019; Omotayo et al. 2021), while their incorporation into maize

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Table 3. The role of endophytic microbes in maize (*Zea mays* L.) plants as bioinoculants in mitigating drought stress

| S/N | Country | Study performed | Endophytic microbes | Outcome | Reference |
|---|---|---|---|---|---|
| 1. | Tehran, Iran | Characterisation of rhizosphere and endophytic bacteria from the roots of irrigated maize (*Zea mays* L.) plants with biotechnological potential in agriculture. | *Bacillus cereus* and *Enterobacter cloacae* | In conclusion, that maize plants irrigated with industrial and municipal wastewater harbour salinity and heavy metals-resistant bacteria, which could serve as potential reservoirs for isolating bacteria capable of alleviating heavy metal stress in plants, reducing heavy metal accumulation in crops like maize, and removing heavy metals from aqueous media (bioremediation of heavy metal-contaminated wastewater systems). | (Abedinzadeh et al. 2019) |
| 2. | Telangan, India | Endophytic bacterial inoculation affects the expression of drought-responsive genes in maize. | *Bacillus* sp. | This study revealed the role of endophytic in alleviating the effect of drought stress in maize plants through regulating plant growth and physiological response. | (Bodhankar et al. 2020) |
| 3. | Islamabad, Pakistan | Interaction of ACC deaminase and antioxidant enzymes to induce drought tolerance in *Enterobacter cloacae* 2WC2 inoculated maize genotypes. | *Enterobacter cloacae* | The involvement of endophytic in reducing the effects of drought stress in maize plants by controlling plant development and physiological response was discovered in this study. | (Maqbool et al. 2021) |
| 4. | Punjab, Pakistan | Inoculation of Bacillus spp. strains under sterile soil conditions ameliorates drought stress in maize (*Zea mays* L.). | *Bacillus* spp. | Differences in the examined biochemical characteristics, lipid peroxidation, and antioxidant responses show that stress alleviation is based on the unique plant–strain interaction. For sustainable agriculture, bacteria like this could be employed to boost crop output and protect plants from biotic and abiotic stress. | (Azeem et al. 2022) |
| 5. | North West Province, South Africa | The structure, diversity, and nutrition routes of bacterial endophytes in maize plants were studied using metagenomic profiling. | | Based on the findings, organic fertilizer may be a beneficial addition to sustainable agriculture methods and should be encouraged, as maize also revealed a slew of new endophytic bacterium families. Therefore, developing ways to isolate and purify this unique endophytic bacterium could aid in the promotion of sustainable agriculture and biotechnology applications should be encouraged in the future. | (Fadiji et al. 2020) |
| 6. | Buenos Aires, Argentina | Inoculation with the bacteria *Azospirillum* sp. and *Herbaspirillum* sp. improves maize's drought resistance. | *Azospirillum brasilense* and *Herbaspirillum seropedicae* | These findings suggest that the bacteria could be employed to assist plants in coping with the harmful consequences of drought stress. | (Curá et al. 2017) |
| 7. | Faisalaba, Pakistan | Exploring the potential of seed endophytic bacteria to improve maize drought stress resistance (*Zea mays* L.) | | The study shows that when seed endophytic bacteria were inoculated under drought circumstances, antioxidant enzymes were dramatically reduced at a *P*-value of 0.05. | (Siddique et al. 2022) |
| 8. | North-West University, Mmabatho, South Africa | Actinomycetes isolates were characterised for plant growth-promoting characteristics and their impact on maize drought tolerance | *Arthrobacter arilaitensis* and *Streptomyces pseudovenezuelae* | The results of this study imply that these isolates are valuable tools that could be converted into bioinoculants to improve plant drought resistance. | (Chukwuneme et al. 2020a) |

ACC – 1-aminocyclopropane-1-carboxylic acid

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crop production as a key player is a cost-effective option considering its effectiveness and proven efficacy (Chukwuneme et al. 2021).

## CONCLUSION

Drought stress mostly leads to a considerable loss in plant growth and crop yield by obstructing the different biochemical, morphological, and physiological processes in the maize plant. Its period of exposure, severity, and stage of growth are part of the elements that prompt the losses in the maize yield. Water deficits due to the consequences of climate change including a decline in rainfall as well as increased dry spells has given rise to drought stress conditions. Drought stress effects on maize plants are evident in their morphology, physio-biochemical as well as molecular characteristics. As such, it is pertinent to utilise proven strategies that can enhance the tolerance and resistance levels in maize plants to ensure an improvement in their growth under drought stress for food security. The utilisation of plant growth-promoting rhizobacteria into drought-stressed soil enhances the stress tolerance in maize plants while providing a cost-effective avenue for sustainable crop health and yields. In reality, research has shown that plant growth-promoting rhizobacteria and endophytic bacteria are used to increase the maize variety production in several nations, and they are often treated through seed inoculation or seed treatment. In the future, there is a need to examine the dynamics of rhizobacteria and endophytic bacteria strains to further comprehend the mechanisms by which they can alleviate drought stress in different maize varieties, especially in developing countries like South Africa.

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