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Chapter

Morpho-Physiological Mechanisms of Maize for Drought Tolerance

Abu Sayeed Md. Hasibuzzaman, Farzana Akter, Shamim Ara Bagum, Nilima Hossain, Tahmina Akter and M. Shalim Uddin

Abstract

Maize is one of the mostly consumed grains in the world. It possesses a greater potentiality of being an alternative to rice and wheat in the near future. In field condition, maize encounters abiotic stresses like salinity, drought, water logging, cold, heat, etc. Physiology and production of maize are largely affected by drought. Drought has become a prime cause of agricultural disaster because of the major occurrence records of the last few decades. It leads to immense losses in plant growth (plant height and stem), water relations (relative water content), gas exchange (photosynthesis, stomatal conductance, and transpiration rate), and nutrient levels in maize. To mitigate the effect of stress, plant retreats by using multiple morphological, molecular, and physiological mechanisms. Maize alters its physiological processes like photosynthesis, oxidoreductase activities, carbohydrate metabolism, nutrient metabolism, and other drought-responsive pathways in response to drought. Synthesis of some chemicals like proline, abscisic acid (ABA), different phenolic compounds, etc. helps to fight against stress. Inoculation of plant growth-promoting rhizobacteria (PGPR) can result to the gene expression involved in the biosynthesis of abscisic acid which also helps to resist drought. Moreover, adaptation to drought and heat stress is positively influenced by the activity of chaperone proteins and proteases, protein that responds to ethylene and ripening. Some modifications generated by clustered regularly interspaced short palindromic repeat (CRISPR)-Cas9 are able to improve maize yield in drought. Forward and reverse genetics and functional and comparative genomics are being implemented now to overcome stress conditions like drought. Maize response to drought is a multifarious physiological and biochemical process. Applying data synthesis approach, this study aims toward better demonstration of its consequences to provide critical information on maize tolerance along with minimizing yield loss.

Keywords: abiotic stresses, osmotic adjustment, stomatal conductance, genomics, transpiration efficiency

1. Introduction

Maize being a main source of food, fodder, and fuel possesses great yield potentiality and nutritional value. It is the most widely produced cereal around the world which is an emerging crop throughout the world. Farmers are interested to its cultivation due to its higher benefit. Since agriculture is mainly reliant on nature/ environment, like most of the cereal crops on which the world population depends, maize productivity is threatened by versatile stresses during its life cycle. Not only production of maize but also world's food security is at stake due to the adversities of abiotic stresses.

World food security is being challenged continuously by numerous abiotic stresses which are the consequences of exhausting climatic change in the recent decades. Abiotic stresses like salinity, drought, flooding, metal toxicity, nutrient deficiency, high temperature, and low temperature can limit the scope of crop choice as well as cause total productivity loss in severe cases. Among all other stresses, water scarcity or drought becomes an important restricting factor for crop production. According to Kramer and Boyer [1], around 28% of the world's land is too dry to support vegetation. For example, Bangladesh is one of the countries subjected to the detrimental influences of climate shifting, where 41 to 50% of land encounters a threat to experience drought each year with increased intensity (IPCC, 2013). To compete with the engrossing amount of drought stress, plants have developed a series of morphological, biochemical, physiological, cellular, and molecular mechanisms [2]. The mechanism involved in drought resistance in plants is either dehydration avoidance or dehydration tolerance [3]. In the first case, plants maintain an elevated water status during drought stress, whereas in the second case, plants function normally with a limited water condition [4].

In recent times, improved maize yield has been attained gradually, although its sensitivity to different abiotic stresses including drought has also increased. Drought being a major abiotic constraint to crop productivity as well as plant growth and development [5] can cause nearly 70% potential yield loss across the world largely because of changing climate [6]. Alike other crops, drought stress hampers maize plants in different biological, biochemical, and molecular aspects. Plants' answer to dehydration stress is somewhat very complex. Various elements which affect this response comprise environment, genotype, plant growth and development stage, and the severity and extent of the stress [7]. As maize is cultivated in over 170 million hectares in the world and is considered the second most important staple crop (FAO statistical database, http://faostat3.fao.org/home/E), it is very important to understand the mechanism behind drought adaptation in maize. Not only this but also the drought tolerance is also a prerequisite to sustain productivity of the plant. So, understanding the drought tolerance is very crucial for food security.

2. Effects of drought on growth and development of maize

Maize is prone to drought almost in every growth stage of its life cycle (**Table 1**), specifically during the reproductive stage [19]. Development and grain yield of maize are not only affected by the severity of drought stress but also by the growth stage of at which the plant is revealed to that stress; treatments of mild and severe drought stress can decrease final grain yield up to 63 and 85% [20]. At pre-anthesis and grain-filling stage, maize is more sensitive, but at seedling stage, drought can also become devastating [14]. Generally, late vegetative and anthesis growth stages have more water requirement than the seedling stage [21]. Drought condition during the seedling stage can cause harmful impact on the early crop establishment and grain yield potential due to premature tasseling which leads to extended anthesis to silk interval [13]. Even total biomass accumulation can be reduced in different developmental stages like 37% at silking stage, 34% at grain-filling, and 21% at maturity period (**Figure 1**) [22].

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Feature	Effect of drought	Source
Morphological	Reduces leaf size, stem growth, and root proliferation	[8]
-	Increased frequency of kernel abortion during pollination	[9, 10]
-	Leaf rolling, stomata closure	[11]
-	Reduced flowering, leaf number, biomass, and seed weight	[5]
	Delayed silking	[12]
	Premature flowering and longer anthesis-silk interval	[13]
Biological	Membrane damage and upset the activity of various enzymes	[14]
	Suppressed photosynthesis, carbohydrate metabolism, and energy metabolism	
Physiological	Unbalance plant-water relations and minimizes water-use efficiency	[14]
-	Significantly inhibited photosynthetic rate	
-	Reduced CO_2 assimilation by leaves is mainly due to stomatal closure, especially those of CO_2 fixation and adenosine triphosphate synthesis	
Biochemical	Malondialdehyde (MDA) accumulation as a biomarker for oxidative stress	[15]
-	Antioxidant accumulation, reactive oxygen species (ROS) scavenging, and transcription activation	[16]
-	Proline accumulation	[17]
-	Higher activity of nonenzymatic antioxidants like β -carotene, ascorbate (ASC), α -tocopherol, reduced glutathione (GSH), carotenoid, enzymes include superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxid (APX), catalase (CAT), polyphenol oxidase (PPO), and glutathione reductase (GR)	[18]

Table 1.

Negative impacts of drought in maize.



Figure 1.

Schematic representation of yield losses in maize due to drought [22–24].

3. Morpho-physiological mechanisms of drought tolerance

To fight against drought stress, plants have advanced multifarious adaptive mechanisms, comprising morphological, physiological, and biochemical adjustment, regulating transcription and gene expression, along with epigenetic plasticity [25, 26]. The most important mechanisms include enhanced water uptake along with prolific and deep root systems, partial water loss by increased diffusive resistance, and reducing leaf size making them succulent in order to decrease the transpirational loss. Potassium ions help in osmotic adjustment (OA); silicon improves the cell water balance and increases root endodermal silicification. Osmolytes with low molecular weight, like proline, glycinebetaine and other organic acids, amino acids, and polyols, are essential to maintain cellular functions while encountering drought. Different plant growth substances such as auxins, gibberellins, cytokinin, salicylic acid, and abscisic acid (ABA) regulate the plant responses toward drought [8].

3.1 Morphological mechanisms of drought tolerance

3.1.1 Leaf rolling and stomatal conductance

Water-deficient condition brings about harmful impacts on whole plant morphology. Cell and leaves undergo tremendous change in drought stress. Reduced leaves per plant, individual leaf size, and leaf area result in decreased photosynthesis [27]. Leaf senescence and rolling also indicate impacts of water deficiency in plants [28]. Thus, water stress adversely affects maize plants causing downgraded fresh and dry biomass production [29].

Stomatal resistance, relative water content (RWC), transpiration rate, leaf-water potential, and leaf and canopy temperature are important characteristics influencing plant-water relations. RWC highlights the water status in plant. It is the most useful index for drought tolerance in plants which reflects the metabolic activity in tissues [17]. Reduction in relative water content as a reply to drought stress has already been noticed in wide range of plants [30]. When plants are subjected to drought stress, they exhibit substantial decrease of leaf-water potential, relative water content, and transpiration rate [31].

3.1.2 Root characteristics

Maize root growth is not inhibited considerably in water stress [32]. Generally, in drought condition, the root and shoot ratio increases because of roots being less sensitive to growth retardation by low water potentials than shoots [33]. While undergoing drought condition, roots induce a signal flowing toward the shoots via xylem which causes physiological changes. Eventually this determines the level of plant adaptation to the stress. Drought induced root-to-leaf signaling flows through the transpiration stream resulting in the stomatal closure, which is an important alteration to reduced water supply [17]. Ethylene, cytokinin, abscisic acid, malate, and other factors are associated in the root-to-shoot signaling process. ABA endorses the K⁺ ion from the guard cells, resulting in loss of turgor pressure which leads to stomatal closure. Loss of cell turgor due to dehydration of plants can increase ABA level up to 50 times [34].

3.2 Physiological mechanisms of drought tolerance

3.2.1 Osmotic adjustment, dehydration tolerance, and transpiration efficiency

Osmotic adjustment means the active accumulation of organic solutes in the plant tissue as a consequence of water-deficient condition or drought stress. This has been regarded as an important physiological adapting mechanism associated with drought tolerance which has gained significance in recent years. Through osmotic adjustment, cytoplasmic and organelle activities occur at normal rate and assist plants to better growth, photosynthesis, and partitioning assimilates [17].

Maintaining cell turgor by reduced water potential, OA regulates photosynthesis and stomatal conductance at lower water potentials, improved root growth and water extraction, delayed leaf senescence and death, and reduced flower abortion which is crucial in dehydration tolerance [35].

3.2.2 Solute accumulation and storage sugar

Osmotic adjustment is involved in accumulating different solutes depending on the rate of drought stress. To maintain cell turgor, various organic and inorganic solutes are accumulated in the cytosol to lessen osmotic potential [36]. According to Hessini et al. [37], these accumulated compounds facilitate stressed cells either by functioning as cytoplasmic osmolytes which improve moisture uptake and preservation or by protecting and stabilizing biomolecules and their structures (i.e., proteins, membranes, chloroplasts, and liposomes) from damage caused by stress condition. Compatible solutes like amino acids such as proline or glycinebetaine, sugars, sugar alcohols (like mannitol and other low molecular weight metabolites), glycerol, and polyols can also be helpful in this process [38].

Balancing of leaf turgor pressure can be achieved by osmotic fine-tuning in drought through deposition of soluble carbohydrates, sucrose, proline, glycinebetaine, and other solutes in cytoplasm to improve water uptake. In water-deficit condition, proline accumulation is the first response of plants, which is the most widely studied due to its substantial significance in stress tolerance by reducing injury to cells. During signaling process, proline can modify mitochondrial functions, stimulate cell proliferation or cell death, and trigger some genic expression, which is ultimately essential for plant's recovery from drought stress [39]. It also helps to stabilize subcellular structures and take part in scavenging free radicals and buffering cellular redox potential during stress conditions [40].

3.2.3 Stay green (SG)/non-senescence

Stay green is an indicator of good plant health especially in drought conditions, which leads to reduced senescence, adaptability to stalk lodging, and post-flowering dehydration. This trait ensures superiority of plants compared to non-stay-green ones [41]. When green plant tissue area contributes more than the average of total plant area, and the grain moisture is lower or equal to the population average, that plants are regarded as stay green [42]. Swanckaert et al. [43] found that maize SG genotypes have higher photosynthetic capacity values with increased values for the proxies. Though an increased photosynthetic capability is not related with more assimilate accumulation in leaves, the stay-green trait was considered as a cosmetic SG. In maize this trait influenced N dynamics as the lower translocation of N from leaves resulted in low nitrogen concentration in the ear which consequently leaded to lower grain dry matter yield. SG trait generally causes changes in the partitioning of dry matter and nitrogen balance between both vegetative and reproductive tissues; the energy source also converts into cell wall material from starch (from ear source).

4. Functional genomics of drought tolerance

Different genes are translated and expressed in water-deficient condition or drought stress. The existing genotypes containing drought-inducible genes

recommend the complex nature of plants in response to drought [26]. Studies executed to understand the molecular mechanisms of drought tolerance have identified some species-specific and conserved genes expressed in stress condition (Table 2) [55]. Additionally, transcription factors that regulate adaptive response in drought stress, such as myeloblastosis (MYB), dehydration responsive element binding (DREB), C-repeat binding factor (CBF), abscisic acid responsive elements binding factor (ABF), ABRE binding (AREB), (NAM, ATAF1/2, and CUC2 containing proteins) (NAC), WRKY, and SNF1-related kinase 2 (SnRK2), were also identified [56, 57]. In spite of these accomplishments, the gene network responsible for drought stress tolerance is still not fully revealed. Nowadays, bio-protective effects are being investigated in different ways to mitigate the crop losses caused due to drought. According to Cura et al. [53], plant growth-promoting rhizobacteria (PGPR), A. brasilense, strain SP-7, and H. seropedicae, strain Z-152, help plants to cope with the adverse effects of dehydration stress. Maize plants inoculated with these bacteria under drought condition resulted into higher carbon, nitrogen, and chlorophyll levels, higher biomass, and lower levels of ethylene and abscisic acid, plant growth-regulating hormones that affect the response toward stress. Less injuries to the cell membrane occur in the bacteria-inoculated plants than the non-inoculated plants in control condition, in the same levels of oxidative stress. Recently different genome editing tools are being applied like zinc-finger nucleases (ZFN), meganucleases, transcription activator-like effector nucleases (TALEN), and the clustered regularly interspaced short palindromic repeat (CRISPR)/CRISPR-associated nuclease protein (Cas) system which have provided the scope of modification to the desired genes in plants [58].

Gene for drought tolerance	Functions	Source
ZmVPP1	Enhanced activity Increased root growth and development	[44]
ZmNAC111	Expresses in transgenic maize Enhances drought tolerance	[45]
ZmPP2C-A10	Helps in abscisic acid signaling	[46]
ZmWRKY40	Regulate the stress-related genes as well as the reactive oxygen species (ROS) content in transgenic lines. ROS is reduced by enhancing the activities of peroxide dismutase (POD) and catalase (CAT)	[47]
MYB gene, ZmMYB3R	Elevated catalase (CAT), peroxidase (POD) and superoxide dismutase (SOD) enzyme activities, increased sensitivity to ABA, and regulation of the stomatal aperture	[48]
ASR gene ZmASR3	Lower MDA levels and higher relative water content and proline content	[49]
Maize glossy6 (gl6)	By involving GL6 protein in trafficking intracellular cuticular waxes, opening the door through which cuticular wax is transported from the site of biosynthesis to the plasma membrane	[50]
Late embryogenesis abundant (LEA) gene ZmLEA14tv	Enhanced the seed germination and survival rate	[51]
ARGOS8	Increased grain yield	[52]
ZmVP14	Biosynthesis of abscisic acid	[53]
ZmCIPK8	Involved in ABA and H2O2 signaling	[54]

Table 2.

Different genes which contribute in maize drought tolerance.

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CRISPR-Cas9 system is easier to execute and very efficient. The system includes a Cas9 endonuclease which is derived from *Streptococcus pyogenes* and a chimeric single guide RNA. This leads Cas9 to a target sequence of DNA in the genome. CRISPR-Cas9 genome editing is undertaken by launching a DNA double-strand break via Cas9 in the target locus [52]. In order to resolve the molecular mechanisms underlying behind drought stress tolerance, comparative physiological and transcriptome analyses on dehydration-tolerant maize (*Zea mays* L.) are being done. Using an RNA sequencing (RNA-seq)-based approach, differentially expressed genes (DEGs) are being identified. From the critical sets of DEGs, specific droughtresponsive genes are being mined out which are primarily associated with nitrogen metabolism, ribosome pathway, and amino acid biosynthesis pathways [11]. The tolerant genes can be associated with stress signal transduction; cellular redox homeostasis maintenance; MYB, NAC, WRKY, and PLATZ transcriptional factor modulated; carbohydrate synthesis and cell wall remodeling; amino acid biosynthesis; and protein ubiquitination processes.

5. Proteomics of drought tolerance

Alike some genes, several proteins are also translated in water-deficit condition; majority of the proteins are water soluble, which contribute to stress tolerance by hydrating various cellular structures [59]. In different studies, membrane-stabilizing proteins have been found to be drought responsive such as dehydrins, ABAresponsive proteins, phospholipase D, glyoxalase I or glutathione-S-transferase [60], and late embryogenic abundant proteins (LEA), increasing water-binding capacity of cells [55]. Transmembrane proteins like AQPs are found to be of vital significance to all stages of plant growth and development under osmotic stress induced by drought, through maintaining cell turgor pressure [61]. Proline accumulation has been found to be correlated with stress tolerance, which preserves the structure of complex proteins, maintains membrane integrity influencing protein solvation under dehydrated condition, and reduces oxidation of lipid membranes [62]. Heat shock proteins (HSPs) (**Table 3**) play a major role in stabilizing protein structure, which are chiefly involved in unwinding few folded proteins and averting protein denaturation under abiotic stress conditions [47, 68].

Maize CIPK gene ZmCIPK8, having a 1356 bp coding region, encodes a polypeptide of 451 amino acids. ZmCIPK8 protein contains two domains which are C-terminal regulatory domain and N-terminal protein kinase domain with a CBL-interacting NAF/FISL motif. They operate by cooperating with some

Protein	Function	Source
Hsp70	In chloroplast, mitochondria, endoplasmic reticulum, and cytosol, it prevents the aggregation and assists in refolding, protein import and translocation, signal transduction, and transcriptional activation	[63]
Chaperonin/Hsp60	In chloroplast, mitochondria, and cytosol, folding and assistance in refolding	[64]
Hsp90	In chloroplast, mitochondria, endoplasmic reticulum, and cytosol, it facilitates maturation of signaling molecules, genetic buffering	[65]
Hsp100/Clp	In cytosol and mitochondria, disaggregation, unfolding	[66]
sHsp	In chloroplast, mitochondria, endoplasmic reticulum, membrane, and cytosol, it prevents aggregation and stabilizes non-native proteins	[67]

 Table 3.

 Proteins related to drought tolerance in maize.

membrane-localized proteins as their targets resulting in higher activity of SOD, which is a major antioxidant enzyme, scavenging superoxide radicals [69] as well as lowering the levels of MDA under drought stress [54].

6. Breeding for drought tolerance

Breeding of drought-tolerant crops implies to fulfill the requirement of the expanding population around the world which will need more food, fodder, and fuel in a defensible way. Advancement in crops drought tolerance is eventually assessed by the increment of grain yield under water-deficient conditions. As it's difficult to predict the exact moment that drought will occur, effective and longacting solutions must be brought up by the agriculturists. The metabolic systems and physiological activities responsible behind drought tolerance are very complex and often hard to allocate. The resistance to drought can be obtained by three different ways which are dehydration escape, dehydration avoidance, and dehydration tolerance [15]. Relevant morpho-physiological attributes include resistance to short anthesis-silking interval, plant wilting, deep root systems, rapid maturity, waxy cuticle, heavy glaucousness or dense pubescence, leaf-water retention, stay-green characteristics, osmotic adjustment, cellular membrane stability, and high harvest index, as well as biochemical traits like long-distance signals provided by plant hormones, abscisic acid, xylem sap pH, and inorganic ions that provide shoot water retention ability, etc. Traits can be improved through pedigree breeding, backcross breeding, bulk population breeding, and recurrent selection [70]. Strategies such as mass screening, marker-assisted selection, as well as genetic engineering can be adapted to attain drought resistance in plants. Maize breeding for drought resistance is prospective by utilizing the existing genetic resources and application of precise phenotyping and breeding informatics, introducing drought-resistance genes [71]. Moreover, for breeding drought-tolerant crops, CRISPR-Cas9 system is generating unique allelic variation [52].

7. Conclusion

Stress tolerance is a complex trait. Different plants adapt themselves differently to tolerate the adversity of stress. Maize as an important cereal exhibits some evidence of stress tolerance, especially drought stress tolerance. Inherently maize changes its morphological structures and physiological activities to mitigate the negative impact of drought. But, to do this the crop fails to produce yields with maximum potential. In this case, breeding for drought tolerance in maize opens a door to achieve higher yield under drought condition. So, more efforts are required to develop maize variety that can tolerate drought stress.

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