

# Drought Stress Signaling in Plants

Subjects: Plant Sciences

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Drought stress restricts plant growth and development by altering metabolic activity and biological functions. However, plants have evolved several cellular and molecular mechanisms to overcome drought stress. Drought tolerance is a multiplex trait involving the activation of signaling mechanisms and differentially expressed molecular responses. Broadly, drought tolerance comprises two steps: stress sensing/signaling and activation of various parallel stress responses (including physiological, molecular, and biochemical mechanisms) in plants. At the cellular level, drought induces oxidative stress by overproduction of reactive oxygen species (ROS), ultimately causing the cell membrane to rupture and stimulating various stress signaling pathways (ROS, mitogen-activated-protein-kinase,  $\text{Ca}^{2+}$ , and hormone-mediated signaling). Drought-induced transcription factors activation and abscisic acid concentration co-ordinate the stress signaling and responses in cotton. The key responses against drought stress, are root development, stomatal closure, photosynthesis, hormone production, and ROS scavenging. The genetic basis, quantitative trait loci and genes of cotton drought tolerance are presented as examples of genetic resources in plants. Sustainable genetic improvements could be achieved through functional genomic approaches and genome modification techniques such as the CRISPR/Cas9 system aid the characterization of genes, sorted out from stress-related candidate single nucleotide polymorphisms, quantitative trait loci, and genes. Exploration of the genetic basis for superior candidate genes linked to stress physiology can be facilitated by integrated functional genomic approaches. We propose a third-generation sequencing approach coupled with genome-wide studies and functional genomic tools, including a comparative sequenced data (transcriptomics, proteomics, and epigenomic) analysis, which offer a platform to identify and characterize novel genes. This will provide information for better understanding the complex stress cellular biology of plants.

Keywords: cellular stress signaling ; drought stress responses

## 1. Introduction

Global warming and climate change adversely affect agricultural production. Erosion of genetic diversity for drought tolerance in major crops is a threat to food security. Abiotic stresses are major threats, and collectively led to 73% decline in cotton production worldwide <sup>[1]</sup>. Drought refers to low water availability for the long-period of time, and affects crop production <sup>[2]</sup>. Drought tolerance is a complex trait involving multiple genes associated with cellular signaling pathways which modify several physio-morphological, and molecular responses. Plant cell membranes perceive stress signals and stimulate various self-activated and hormone-dependent signaling mechanisms <sup>[3]</sup>. Mitogen-activated-protein-kinase (MAPK) networks are involved in stress signaling and activate several stress-responsive proteins <sup>[4]</sup>. In stress signaling pathways, calcium ( $\text{Ca}^{2+}$ ) is a common second messenger, controls many physiological processes in plants. The cytoplasmic  $\text{Ca}^{2+}$  concentration varies in response to drought stress and various hormones such as abscisic acid (ABA), jasmonic acid (JA), and ethylene <sup>[5]</sup>. Under high concentrations, ABA interacts with SnRK2 proteins, which subsequently initiate molecular and physiological responses to drought stress <sup>[6][7][8]</sup>. Jasmonic acid (JA) and its derivatives also activate signaling pathways similar to ABA <sup>[9]</sup>. Overproduction of reactive oxygen species (ROS) also triggers defense mechanisms and excessive amounts of ROS scavenged by enzymatic and non-enzymatic defense machinery in plants <sup>[10]</sup>.

Following the successful transduction of stress signals, plants actively adopt drought recovery mechanisms. Tolerant plants are able to resume growth and overcome the growth deficit induced by drought. Cotton has developed numerous morpho-physiological approaches, such as photosynthetic response <sup>[11]</sup>, osmotic adjustment, stomatal regulation, low leaf water loss, high relative water contents (RWC), and enlarged tap roots <sup>[12]</sup>. These features contribute to drought tolerance through a multigenic effect. Genetic statistics and improvements of physio-morphological characters are important to reduce the effects of drought. Alterations in physio-morphological and biochemical traits have vital roles in maintaining favorable water balance in plant cells and tissues.

Genome modification technologies and transgenic approaches have been employed to develop drought-tolerant crops overexpressing transgenes that are important for plant physiology. Targeted genome editing with the CRISPR/Cas9 system has been utilized to modify the genome to obtain more stable and heritable mutations [13]. Genome-wide studies have been performed to explore stress-related candidate regions and genes for drought tolerance. Various drought-related quantitative trait loci (QTL) clusters and hotspots have been mapped in cotton. Several QTLs for abiotic stress, especially drought, have been identified using single nucleotide polymorphisms (SNPs) in genome-wide association studies (GWAS). Meta-analyses can be performed to identify common QTLs for drought-related traits [2]. Whole genome sequencing and re-sequencing of allotetraploid and diploid cotton species provide information in the biologically active states of DNA [14]. Fine- and high-density genetic maps, transcript abundance, epigenetic modifications, and SNP array platforms can also be used, as reported for other model plants (rice and *Arabidopsis*). These approaches serve as a platform for gene mapping, isolation, and cloning for drought tolerance. Moreover, the identification of novel genes can be facilitated by high-throughput marker development for stress tolerance in plants.

This review focuses on the cellular and molecular signaling networks and drought coping adaptations in plants to overcome the impact of drought stress. The use of functional genomics to overcome drought stress is also discussed. Furthermore, this review provides an overview of the genetic basis of drought tolerance in cotton, with a focus on QTLs and candidate abiotic stress tolerance genes in cotton, which might be employed for novel cotton breeding in the future.

## 2. Role of TFs in Drought Stress Signaling Pathways

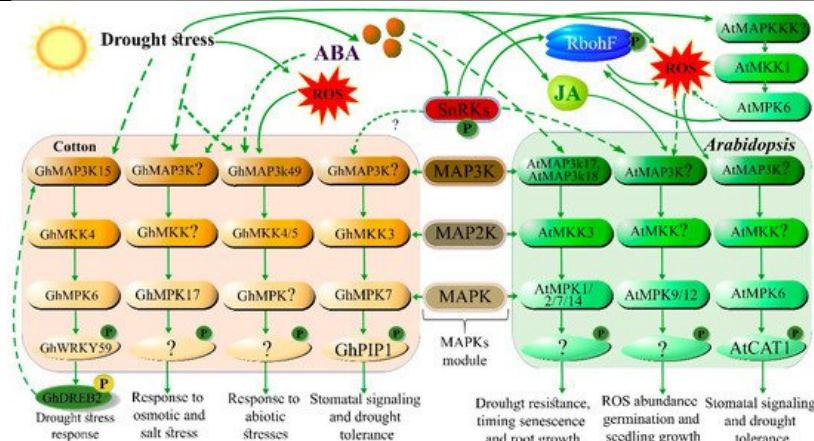
TFs are the principal regulatory elements for many genes involved in environmental stress responses. TFs have vital roles in signaling pathways, from signal reception to the expression of genes related to drought stress in plants. Genes contain *cis*-acting components in their promoter regions, which serve as binding sites for TFs to regulate gene expression in signal transduction pathways. Signaling cascades in networks responsive to drought stress are activated via TFs that work together to induce drought tolerance [15]. Approximately, 1500 TFs are involved in the expression of stress related genes in *Arabidopsis* [16]. Several transcription factor families like MYB, WRKY, ERF, NAC, and bZIP have been characterized and shown to be useful tools for enhancing drought tolerance in plants. In recent studies, TFs involved in stress tolerance were identified in cotton and *Arabidopsis* (Table 1). Overexpression of *GhABF2* in cotton enhanced the activities of catalase (CAT) and superoxide dismutase (SOD), and improved yield in transgenic plants [17]. Another TF related to R2R3-type MYB, *GbMYB5*, responded positively to drought stress [18]. Ectopic expression of the *GhWRKY41* gene in tobacco plants led to increased activity of antioxidant enzymes, lower MDA content, increased stomatal closure, and upregulation of antioxidant-related genes [19]. In *Gossypium barbadense*, a R2R3-type *GbMYB5* TF gene enhanced drought tolerance in transgenic tobacco and cotton. These results suggest the involvement of *GbMYB5* in adaptive drought stress responses [18]. *GhWRKY59* is an important TF that ensures drought tolerance in cotton (Figure 1) [20]. In Upland Cotton, a NAM domain gene termed *GhNAC79*, improves drought tolerance, and also responds to JA and ethylene treatments. Additionally, its overexpression improved stress tolerance in *Arabidopsis* and cotton [21].

**Table 1.** Key genes involved in abiotic stress signaling in cotton.

Gene	Type	Phenotypic Effect/Function	Reference
<i>GhHUB2</i>	Histone H2B monoubiquitinatin E3 ligase encoding gene	Drought tolerance through increased soluble sugar, proline, and leaf relative water contents	[22]
<i>GrMAPKKK</i> and <i>GhMAPKKK</i>	MAPK gene family	Drought and salt responsive	[23]
<i>GhMAP3K1</i> , <i>GhMCK4</i> , and <i>GhMPK6</i>	MAPK signaling gene	Regulates the drought stress response by interacting with <i>GhWRKY59–GhDREB2</i>	[20]
<i>GhMCK3</i>	MAPK signaling gene	Enhanced drought tolerance	[24]
<i>GhMAP3K40</i>	MAPK signaling gene	Salt and drought stress tolerance at the germination stage	[25]
<i>GhMPK4</i>	MAPK signaling gene	Increased sensitivity to ABA, salt, and drought	[26]
<i>GhMPK17</i>	MAPK signaling gene	Osmotic and salt stress tolerance	[27]
<i>GbMPK3</i>	MAPK signaling gene	Enhanced oxidative and drought stress tolerance	[28]
<i>GhMPK6a</i>	MAPK signaling gene	Drought and salinity	[29]

Gene	Type	Phenotypic Effect/Function	Reference
<i>GhMKK1</i>	MAPK signaling gene	Drought and salinity	[30]
<i>GhMKK5</i>	MAPK signaling gene	Drought and salinity	[31]
<i>GhMPK2</i>	MAPK signaling gene	Drought and salinity	[32]
<i>GbRLK</i>	Receptor-like kinase	Drought and salinity	[33]
<i>GaHDG11 (HD-ZIP)</i>	Transcription factor	Drought and heat stress	[34]
<i>GhNAC79</i>	Transcription factor	Improves resistance to drought stress	[21]
<i>GhERF38</i>	Transcription factor	Drought, abscisic acid, and salinity	[35]
<i>GhERF2, GhERF3, GhERF6</i>	Transcription factor	Drought, salt, ethylene, and abscisic acid	[36]
<i>GhWRKY59</i>	Transcription factor	Activates MAPK signaling gene under drought	[20]
<i>GhWRKY25</i>	Transcription factor	Drought and salinity	[37]
<i>GhABF2 (bZIP)</i>	Transcription factor	Enhances the activities of CAT and SOD, regulates gene expression related to ABA	[17]
<i>GhNAC2</i>	Transcription factor	Longer roots, and enhanced salt and drought tolerance	[38]
<i>GhCBF3, GhAREB1, and GhAREB2</i>	ABA-induced gene	Small stomatal aperture, enhanced drought- and high salinity-tolerance via the ABA signaling pathway	[39]
<i>GhNAC7-GhNAC13</i>	Transcription factor	Cold, abscisic acid, drought, and salinity	[40]
<i>GbMYB5</i>	Transcription factor	Reduced water loss through stomatal conductance, and increased proline content and antioxidant enzymes	[41]
<i>GhWRKY41</i>	Transcription factor	Lower malondialdehyde content, higher antioxidant activity, and induced stomatal conductance	[19]
<i>GhWRKY17</i>	Transcription factor	Increases sensitivity to ABA and drought stress	[42]
<i>GhNAC8-GhNAC17</i>	Transcription factor	Drought, salinity, cold, and ABA	[43]
<i>GhNAC1-GhNAC6</i>	Transcription factor	Drought, cold, salinity, and ABA	[44]
<i>GhDREB</i>	Transcription factor	Drought, cold, and salinity	[45]
<i>GhDREB1</i>	Transcription factor	Drought, cold, and salinity	[46]
<i>GhDBP2</i>	Transcription factor	Drought, cold, and ABA	[47]
<i>GhERF1</i>	Transcription factor	ABA production and drought stress signaling regulation	[48]
<i>GhERF4</i>	Transcription factor	ABA production and drought stress signaling regulation	[49]
<i>GhDREB1L</i>	Transcription factor	Drought, cold, and salinity	[50]
<i>GhPYL9–11A</i>	ABA receptor gene	ABA receptor that mediates the response to drought stress	[51]
<i>GhSnRK2</i>	Involved in ABA signaling	Drought, salinity, cold, and ABA	[52]
<i>GhCDPK35, GhCDPK28, GhCDPK16, GhCDPK14, GhCDPK11 and GhCDPK3</i>	Ca <sup>2+</sup> -activated gene	Drought and salinity stress responsive	[7]
<i>GhCIPK6</i>	Ca <sup>2+</sup> -activated gene	Increased drought, salinity, and ABA stress tolerance	[53]
<i>GhD12G207</i>	CDK gene family	Increased concentration of antioxidant enzymes (POD, SOD, and CAT), cell membrane stability, and chlorophyll content under drought and salt stress	[54]

Gene	Type	Phenotypic Effect/Function	Reference
<i>GaMYB62L</i>	Transcription factor	Increased chlorophyll and proline contents, higher germination rate under drought salt stress	[55]
<i>GhTPS11</i>	Functional gene	Drought, heat, salinity, ABA, and gibberellin acid	[56]
<i>GhAVP1</i>	Functional gene	Drought and salinity tolerance	[57]

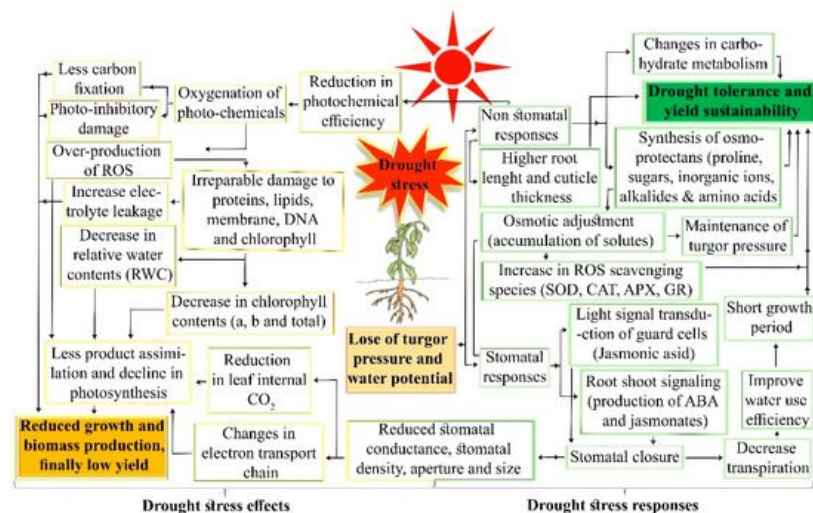


**Figure 1.** Drought-induced, ABA-dependent, ABA-independent MAPK signaling, and interaction between ABA, ROS, and MAPK signaling under drought stress in plants. ABA-regulates various MAPKs in cotton and Arabidopsis. ABA promotes drought sensing and signaling in plants. The different cascades are represented by different color schemes in the figure. Solid arrow lines denote established signaling mechanisms, while dashed arrow lines denote unestablished signaling pathways. ABA-activated SnRK2s trigger and phosphorylate downstream targets, such as respiratory burst oxidase homolog (RBOH) and various MAPKs. Activation of RBOH induces ROS production. ROS signaling and ABA signaling may overlap with MAPK factors, to interact and regulate drought tolerance. MAP3K17/18-MKK3-MPK1/2/7/14 is an ABA-induced complete MAPK cascade involved in stomatal signaling, senescence, and drought tolerance mechanisms in *Arabidopsis*. In addition, MKK1 activates MPK6 to positively regulate CATALASE1 (CAT1) for ROS abundance. In cotton, the drought- and ABA-induced MAPK cascade MKK3-MPK7-PIP1 is associated with stomatal signaling and drought tolerance. Another ABA-mediated MAPK module, MAPKKK49-MKK4/MKK5, is associated with abiotic stress responses. *GhMPK17* gene is a novel, well-characterized MAPK, which is associated with responses to osmotic and salt stresses in cotton. An ABA-independent and drought-mediated MAPK module (MAP3K15-MKK4-MPK6-WRKY59) regulates drought tolerance in cotton. Drought stress triggers the MAPKKK15 cascade, which phosphorylates the WRKY59 transcriptional factor. Interestingly, WRKY59 binds to the promoter of *DREB2* and regulates the expression of drought-sensitive genes. Meanwhile, it positively regulates the expression of *MAP3K15* by establishing a feedback loop, which regulates drought tolerance in cotton.

### 3. Cellular and Molecular Responses to Drought Stress in Plants

Drought stress affects plant growth, leaf and stem dry weights, canopy and root growth, plant height, and the number of nodes in plants. Similarly, some physiological properties, such as stomatal conductance, transpiration rate, photosynthetic rate, and water potential decrease under osmotic stress. Finally, osmotic stress limits the accumulation of dry matter by up to 50% under critical water deficiency [42][58]. These traits are potential candidates for drought tolerance in plants. Genetic improvement on the basis of physio-morphological traits is more important because, these traits have vital roles in maintaining a favorable water balance through stomatal closure, reduced transpiration, high water use efficiency, accumulation of proline, trihalose, and polyamines, leaf rolling, wax content, deep root system, and earliness [59].

After successful transduction of signals and sensing the drought stress, plants initiate drought recovery mechanisms through various physio-morphological and biochemical responses (Figure 2). Plants have developed various mechanisms to minimize or tolerate multiple stresses. Drought tolerance, drought recovery, drought escape, and drought avoidance are the four important categories of drought tolerance tools [40]. Tolerant plants subjected to stressful environments adopt an 'escape scenario' by utilizing energy for defense mechanisms, which eventually impacts growth and production. During drought avoidance, plants reduce transpiration and develop deep and vigorous root systems to increase water uptake to help maintain tissue water potential [60]. Tolerance to drought is the capacity of plants to endure severe dehydration through osmotic adjustment by osmo-protectants [60][61]. Drought recovery is the ability of plants to restart growth and overcome yield deficits following severe stress. Plants have established numerous morpho-physiological adaptations such as root growth, OA, photosynthetic rate, and stomatal regulation to overcome drought stress (Figure 2).



**Figure 2.** Overall pathways of drought stress effects and plant responses to drought stress.

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