

# ALTERATIONS IN TRANSCRIPTOME, PROTEOME AND METABOLOME DURING DROUGHT STRESS IN PLANTS

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**Abstract** – Global climate changes may lead to increased temperature and decreased precipitation in many parts of the world. Sustainable food production is the main challenge to our current agricultural system. At the global level, water stress is one of the most critical abiotic factors that affects crop productivity. Currently, a vast amount of research efforts are being done to generate molecular information leading to an understanding of abiotic stress tolerance in plants. Transcriptome analysis is a cost effective and suitable approach for the identification of candidate genes for adaptive traits and molecular markers that are linked to phenotypic variation under drought. Proteome analysis is helpful in deciphering the cellular processes associated with drought. Although gene expression analysis at the transcription level has enhanced our understanding regarding the response of plants to drought stress, many questions remain unanswered at the protein level. In view of the fact that the plant proteome is highly dynamic in nature, proteomics is becoming essential for the study of many different aspects of plant functions. In plants, water scarcity affects morphological, physiological, and biochemical processes, including carbon assimilation and partitioning, respiration, nutrient uptake, translocation, and whole metabolism. Water deficit primarily affects the cell turgidity and promotes stomatal closure, controlling transpiration rates, and water loss. It will also unavoidably restrict CO<sub>2</sub> supply to photosynthesis, ultimately impairing leaf metabolism and plant growth. Alterations in transcriptome, proteome and metabolome help plant to recover from drought and survive.

## INTRODUCTION

Plants are often permanently exposed to a variety of abiotic stress, such as salinity, drought, heat, and cold. Drought stress is one of the primary abiotic pressure that causes significant losses in agricultural production and it will continue to increase in both intensity and frequency with increasing planet temperature. (Poveda, 2020) Global climate models predict a significant increase in intensity and frequency of hot and dry days (Meehl *et al.*, 2007). Decreased precipitation will lead to more severe drought like events and elevated air temperature accompanying drought invariably leads to advanced plant tissue temperature. This combination results in heat stress due to insufficient water to meet the evaporative demand. Heat and drought pressures negatively affect the yields of main crops including cereals (Osborne *et al.*, 2013),

which are staple foods that account for 60% of the global food energy supply. Despite the frequent occurrence of combined heat and drought episodes under field conditions, the majority of studies involving both model and crop plants have focused on independent heat or drought pressure responses (Song *et al.*, 2020).

### Overall effect of drought on plants

Plants can respond to drought through various ways, such as adaptations in shoot root allocation, growth rate, photosynthetic rate, stomatal conductance, and leaf abscission. Similarly, the above pathway is also reflected in the alterations at plant's molecular level. The study of drought avoidance and tolerance of different trees is helpful in selection of trees for afforestation in arid areas, and lays a theoretical foundation for soil and water conservation and ecological protection (Xu *et al.*,

2022). Genomewide identification of drought responsive regulons in contrasting drought tolerant genotypes will help to unravel systemlevel interplay between different genetic pathways that impart drought tolerance (Lenka *et al.*, 2010). It is very exciting to record and interpret plant response when subjected to abiotic stresses and understand the cross talk that takes place during the stress. The risk that climate alteration poses to food security has intensified the assessment of the impact of combined pressures on plants and several studies focusing on combined heat and drought pressures at the agronomic, physiological, molecular, and metabolic levels have been conducted. When drought pressure occurs, various genes are induced in drought signal transduction, which consists of complex networks of protein–protein reactions, transcription factors (TFs), and promoters (Xu *et al.*, 2020).

The great complexity of plant response to drought makes the task of identifying causal loci, alleles and genes exciting. This is partly due to the fact that plant survival under pressure is multifaceted, with many plant processes directly or indirectly affected by plant water status. Despite the lack of full understanding, numerous studies indicate that both the ephemeral and longerlasting responses to drought pressure are driven by alterations in multiple biosynthetic, transport, signalling and overall metabolic networks (von Wettberg *et al.*, 2018). Determining the mechanisms directly involved in drought tolerance remains an inspiring task because it involves several metabolic and morphologically adaptive pathways. Abscisic acid (ABA) is an important phytohormone involved in drought pressure tolerance in plants and its mechanism of action is also relatively clear. ABA mediated stomatal closure is the mechanism used by plants to adapt to water deficiency. Reactive oxygen species (ROS), including hydrogen peroxide, which are widely generated under pressure, have been proposed to function as second messengers in ABA signalling in guard cells. ABA stimulated ROS accumulation activates plasma membrane calcium channels and triggers stomatal closure (Huang *et al.*, 2015).

During the pressure response, ABA must also mediate crosstalk with other signal pathways to perform its function. For example, ABA activates brassinosteroidintrinsic 2 (BIN2), a negative regulator of brassinosteroidsignaling, by inhibiting ABA INSENSITIVE1 (ABI1) and ABI2mediated

BIN2 dephosphorylation. BIN2 phosphorylates SnRK2s and activates downstream pathways through the central role of SnRK2s in the ABA signalling pathway. ABA activates SnRK2s to phosphorylate ABA responsive kinase substrate 1 (ASK1) to inhibit its transcriptional activity. Then, multiple reactions lead to the inhibition of K<sup>+</sup> influxmediated stomatal opening that promotes stomatal closure in response to ABA. The mitogen activated protein kinase (MAP) cascade also plays an important role in plant drought pressure response. This signalling pathway transmits pressure signals from receptors to specific effectors to regulate gene expression, cell activity and protein function in various developmental and environmental adaptation processes (Li *et al.*, 2022)

Crops facing drought pressure activate the internal defence system to withstand the adverse growth conditions. For instance, antioxidant enzymes, such as peroxidase (POD), catalase (CAT), and superoxide dismutase (SOD), prevent reactive oxygen species (ROS) accumulation. Once the plant's innate defence becomes incapacitated under severe drought pressure, biostimulants such as plant growth regulators are applied to boost plant resistance mechanisms. Melatonin is a plant stimulator that promotes seed germination, root development, and plant growth during unfavorable environmental conditions (Yuan *et al.*, 2022)

### **Alterations in transcriptome under drought condition**

Transcriptome analysis is a costeffective and suitable approach for the identification of candidate genes for adaptive traits and molecular markers that are linked to phenotypic variation under drought (Shanker *et al.*, 2014). Transcriptome sequencing technologies provide a framework dataset for researches related to construction of transcriptome map, determination of metabolic pathways, clarification of gene expression patterns, and mining of new genes (Gong *et al.*, 2015). To explore the molecular regulation mechanisms of plants in response to different stresses, transcriptome analysis has been performed on a variety of crops. Global transcriptome profiling provides highlevel insight into these alterations by facilitating both the qualitative and quantitative estimation of complex behaviour of the responding biological processes. It was demonstrate that, irrespective of water pressure, axes of transcriptome variation mirror species' genetic variation, with high diversity among

wild accessions, significant divergence among wild and cultivated, and limited variation within cultivated species (von Wettberg *et al.*, 2018).

Secondary metabolism pathways such as nicotinate and nicotinamide biosynthesis, alkaloid biosynthesis, monobactam biosynthesis, zeatin, flavonoid and diterpenoid biosynthesis and isoflavonoid, glucosinolate and steroid (sesquiterpenoid and triterpenoid) biosynthesis are activated. Numerous other pathways of potential functional relevance included fatty acid metabolism pathways related to cutin, suberin and wax biosynthesis, linoleic acid and sphingolipid metabolism enriched and circadian rhythm, ascorbate and aldarate metabolism, vesicular transport (SNARE interactions), and plant pathogen interaction enriched. In the abscisic acid dependent pathway, pyrabactin resistance proteins/PYR like proteins/components of ABA receptors (PYR/PYL/RCAR) receive ABA to inhibit type 2C protein phosphatases (PP2Cs), thereby increasing the levels of SNF1 related kinase 2 (SnRK2) to activate TFs such as ABA responsive element binding factors (AREBs), ABA binding factors (ABFs), and myeloblastosis related proteins/ myelocytomatosis related proteins (MYBs/MYCs). In addition, APETALA2/ ethylenes responsive element binding factors (AP/ERF), *Arabidopsis* transcription activation factor (ATAF), no apical meristem proteins (NAC), and zinc finger homeodomain (ZFHD) family members have been determined to be induced under drought in an ABA independent pathway (Liu *et al.*, 2015).

Gibberellic acid (GA) also plays an important role in drought pressure and seed development. The DELLA proteins comprise a class of GA signalling repressors, such as REPRESSOR of gal3 (RGA), GAINSENSITIVE (GAI), RGALIKE1 (RGL1), RGALIKE2 (RGL2), and RGALIKE3 (RGL3) (Chen *et al.*, 2019). Prior studies have shown that DELLA accumulation is linked to growth restriction upon exposure to abiotic pressure and inhibits the accumulation of reactive oxygen species (ROS), which accumulate under biotic and abiotic pressure. Numerous genes were identified during drought and osmotic pressure in diverse plants. Generally, they can be divided into abscisic acid (ABA) dependent and other signalling pathways. ABA is a main phytohormone involved in the drought pressure response in plants; it is involved in stomatal closure and pressure responsive gene expression. Other signaling pathways for drought pressure include osmotic pressure signalling, the

calcium dependent pathway, mitogen activated kinase mediated signalling, phospholipid signalling and reactive oxygen species (ROS) signalling, among others (Wang *et al.*, 2020).

Recently, the genes encoding several Gly Asp Ser Leu (GDSL) proteins, which were named seed fatty acid reducer (SFAR) genes and observed to be down regulated by DELLA proteins, were reported to reduce fatty acid storage in *Arabidopsis* and *Brassica napus* (Karunaratna *et al.*, 2020). Water deficits also affect the biosynthesis and catabolism of several hormones in plant tissues which in turn modulate many physiological processes. For example, during drought pressure, abscisic acid (ABA) and ethylene levels increase, while the levels of gibberellins, auxins and cytokinins decrease. ABA, a well known root to shoot pressure signalling compound controls stomatal closure and the expression of pressure genes during drought, while ethylene functions in leaf abscission (Fig. 1). These processes are important in conserving water and alleviating osmotic pressure damage imposed by drought (Ngara *et al.*, 2021).

The bZIP transcription factor and ABRE binding proteins (AREBs)/ABFs (ABFs) can bind to the ABA response element (ABRE, PyACGTGGC) and activate downstream genes. Indeed, the ABRE element is an enriched motif in promoters of drought responsive genes. *OsMYB2* expression is induced by a variety of stresses and in turn, it enhances the tolerance of transgenic plants to salt, cold and dehydration pressures by regulating accumulation of H<sub>2</sub>O<sub>2</sub> and malondialdehyde as well as the expression of genes involved in proline and ascorbate synthesis (Yang *et al.*, 2012). NAC transcription factors are involved in almost all aspects of plant activities throughout the plant life cycle. Over expression of *OsNAC10* significantly expands the root diameter of transgenic rice and therefore enhances drought tolerance under normal and drought pressure conditions during the reproductive stage. The regulatory networks of the related transcription factors were exhibited well by weighted gene coexpression network analysis (WGCNA) (Li *et al.*, 2012).

#### **Alterations in proteome under drought condition**

Proteomics, which is the study of the structural and functional features of all the proteins in an organism, is an important means of understanding complex biological mechanisms, including plant responses to abiotic pressure tolerance. Using

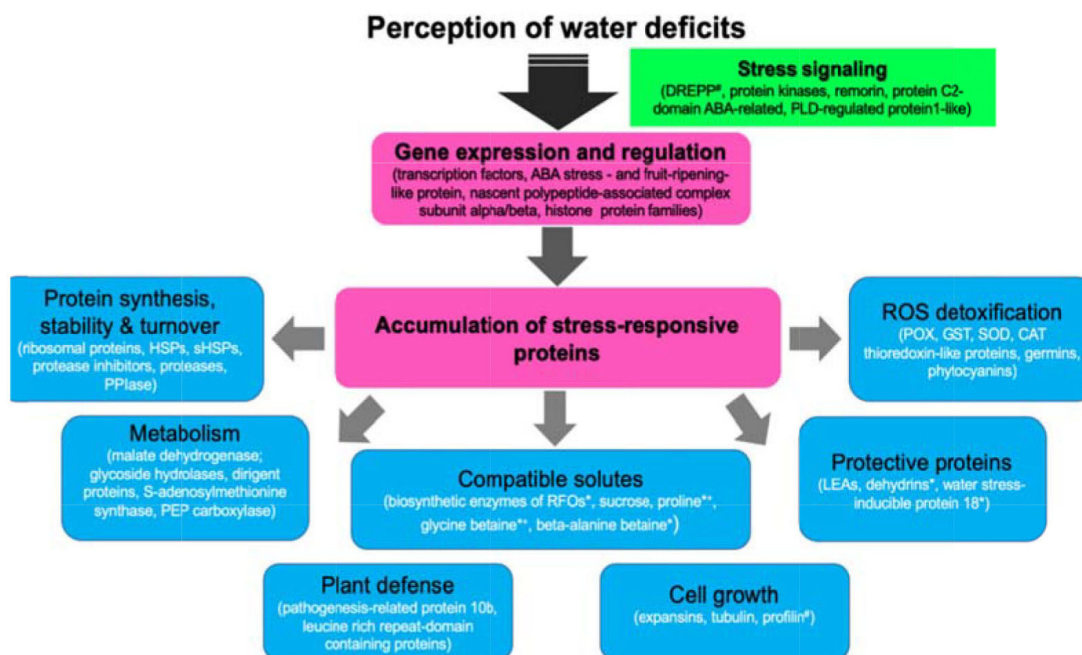


Fig. 1. A generalized molecular response network during droughtstress in sorghum plants (Ngara *et al.*, 2021).

transcriptomic or proteomics sequencing, many genes associated with drought response were identified in a number of plants, such as *Arabidopsis* (Meng *et al.*, 2019). At molecular level, plants react to pressure conditions by changing gene expression levels. Several drought inducible genes have been identified by transcriptome analysis in various plants. Identified genes by these analyses do not always represent the actual dynamics of final gene products, the proteins, because the levels of specific mRNAs do not always correlate well with the levels of proteins. Proteins are key functional effectors of cellular processes. Therefore, to understand their biological system, the molecular characterisation of proteome should be figured out. Proteomic studies offer an occasion to categorise patterns of protein accumulation during stress perception, adaptation and cell defence. Identifying new proteins, determining their expression patterns in drought response and considering their functions would provide the basis of effective engineering strategies to improve crop tolerance to different stresses. Studies highlight that the integrated physiology and proteomic analysis would provide a better insight into the molecular responses of plants during drought (Cevik *et al.*, 2019).

The comparative proteomic analysis of the response to drought stress identified 417 proteins that showed obvious alterations in abundance.

Abiotic pressures such as drought, salinity, heat pressure, and water logging are the main climatic factors for decreasing the growth, development, yield, and quality of crops (Rezaeizadeh *et al.*, 2019). Drought responsive genes encode proteins involved in signalling, gene expression and stress damage control and repair (Lenka *et al.*, 2011). A number of previous studies showed that the reduction in oil content was associated with a decrease in oleic acid and an increase in erucic acid and glucosinolate (Rezaeizadeh *et al.*, 2019). Mohammadi *et al.* (2018) determined that the reduction in oil content was due to a decrease in carbohydrates for oil synthesis and an increase in oil oxidation under drought pressure. The result of the study reflected a decrease in oil content because of drought pressure. It was verified by oil body observations and oil content measurements. The GO and KEGG enrichment analyses showed that the GO terms or pathways associated with fatty acid metabolism were enriched in most DEG or DPLG clusters in the transcriptome and proteome. In fatty acid biosynthesis, the down regulated genes included LEC1 and WRI1, the key regulators that coordinate the expression of fatty acid biosynthesis genes, and FabI, a component of the fatty acid synthase complex that participates in critical process of fatty acid elongation. In fatty acid degradation, acylCoA oxidase (ACX) is the first and most important step controlling enzymes involved

in fatty acid  $\beta$ oxidation (Xin *et al.*, 2019).

MFP2 is a multifunctional peroxisomal isozyme that adds  $H_2O$  over the 2transenoylCoA double bond and oxidizes L3hydroxyacylCoA to 3ketoacylCoA with  $NAD^+$  in  $\beta$ -oxidation. The last step of the  $\beta$ -oxidation cycle requires a KAT enzyme catalyzing fatty ketoacylCoA to produce one acetylCoA molecule. Alcohol dehydrogenase is the first enzyme and a ratelimiting enzyme in the oxidation of fatty acids in peroxide and is a key enzyme involved in the conversion of ethanol into acetaldehyde during the process of fatty acid degradation (Zhang *et al.*, 2021). The proteomic studies in maize and soybean primary roots at low water potential showed increase in reactive oxygen species (ROS) scavenging proteins and region specific regulation of cell wall proteins, phenylpropanoid metabolism and increase in ferritin proteins in the elongation zone (Dalal *et al.*, 2018).

Under longer periods and greater drought severity, the photosynthetic machinery becomes increasingly impaired at the photochemical and biochemical levels due to impacts in pigment pools, photosystems functioning, enzyme activities (namely, ribulose1,5bisphosphate carboxylase/oxygenase, RuBisCO), and membrane integrity. A secondary pressure also occurs, related to an increase in reactive species of oxygen (ROS) and chlorophylls. Nonetheless, given that plants have often evolved under recurrent exposures to drought, they have acquired highly efficient pressure defence systems, involving adjustments at several scales, from the gene to the whole plant level. Plant defence mechanisms include those associated with the strengthening of the antioxidative system, comprising enzymes (e.g., catalase, superoxide dismutase, peroxidase) and nonenzymatic components (e.g., ascorbic acid,  $\alpha$ -tocopherol, RFOs), complemented with thermal dissipation mechanisms (e.g., photoprotective carotenoids) and the cyclic electron flow (CEF) involving proteins of photosystem (PS) I and/or II. Altogether, these response mechanisms contribute to maintain energy balance and cell oxidative homeostasis (Marques *et al.*, 2022). Chaperone synthesis and oxidative pressure tolerance mechanisms allow plants to survive water deficit. Proteome studies have contributed to better understanding of the role of ABA regulation in the synthesis of chloroplast proteins (Shanker *et al.*, 2014).

### Alterations in metabolome under drought condition

Metabolomic techniques have recently been used to investigate the composition of exudates in great detail (van and Bouwmeester, 2016). Important compounds identified in root exudates include organic acids from primary and secondary metabolism (such as oxalate, malate, salicylate, ascorbate, lactate, and citrate), saccharides and their derivatives, and amino acids (Valentinuzzi *et al.*, 2015). Analyses of the metabolic profiles of root exudates have demonstrated great plasticity in metabolite composition linked with abiotic (P and iron soil deficiency) or biotic (interspecific competition) shifts (Valentinuzzi *et al.*, 2015). One study found alterations in the exudate composition of soybean (*Glycine max*) under drought pressure, including an increase in osmolytes (including proline and pinitol), which can assist in the maintenance of cell turgor. Interestingly, there were positive correlations among the composition of exudates and phloem (in relation to organic acids and amino acids) and among exudates and roots (in relation to saccharides) (Canarini *et al.*, 2015). This suggests that drought affects the metabolic profile of the phloem and roots. The altered metabolome may serve to achieve osmotic adjustment within the plant. To the best of our knowledge, however, metabolomic analyses have not been used to study root exudates under multiple levels of water availability and especially under drought pressure and the subsequent recovery. Plant responses to low water availability can affect the concentration, composition, and distribution of both primary (maintaining life processes and facilitate growth) and secondary metabolites (Mundim and Pringle, 2018). However, the role of secondary or specialized metabolism in drought defence and plant adaptation mechanisms has been emphasized. These specialized metabolites can be divided into three main distinct groups: terpenes, phenolics, and nitrogen containing compounds. Water limitation induces different patterns of secondary metabolites accumulation (e.g. terpenoids and phenolics) including increase, reduction or no alteration. This has been attributed to the concentrations of secondary metabolites being specific to the species, the experimental conditions, the class of secondary metabolite and even compound specific (McKiernan *et al.*, 2014).

### Effect on flowering

Flowering time is an important factor determining yield and seed quality in plants. An alteration in flowering time is a strategy used to survive abiotic pressures. Among abiotic pressures, drought can increase anthesis Silking Intervals (ASI) in maize resulting in negative effects. Transcript levels of several genes that have previously been shown to affect flowering time, such as *PRR37*, transcription factor *HY5*, and *CONSTANS*, were significantly altered by drought conditions. Furthermore, several drought responsive transcripts containing C<sub>2</sub>H<sub>2</sub> zinc finger, CCCH, and NAC domains were identified which are frequently involved in transcriptional regulation. They may thus have potential to alter gene expression programs to alter maize flowering time. In response to pressure, such as drought, flowering pathways are accelerated to produce flowers and seeds more rapidly (Krasensky and Jonak, 2012).

Drought pressure has many negative effects, such as decreasing carbon availability flower drop, pollen death, ovule abortion, and the anthesis silking interval (ASI) during the reproductive stages. Drought induced increases in the ASI negatively affect the fertilization rate, kernel filling, and seed quality and weight (Song *et al.*, 2017). Drought pressure disrupts cellular homeostasis and gives rise to morphological, physiological, and molecular alterations. In particular, drought pressure disrupts photosynthesis and transfer of stored carbohydrates into grains during the crop flowering stage, which reduces grain number and weight. This reduction is exacerbated by pressure at the early grain filling stages. In addition, remobilization of stored carbon reserves in wheat is facilitated by water pressure and water deficit during grain filling, which enhances plant senescence and accelerates grain filling (Deng *et al.*, 2018).

### CONCLUSION

It can be concluded from various studies that drought stress alters the transcriptome, proteome as well as metabolome of plants. With the advent of drought like conditions, transcription profile of a plant changes. The genes that were not transcribed earlier are transcribed under the influence of drought. Plant's ability to tolerate drought depends on how early it alters its transcriptome. Changes in transcriptome bring about translation of new proteins that can effectively carry out osmotic

adjustments, scavenging of ROS etc. and save plant from adverse effects of drought. Changes in metabolites during drought compliments plant's survival rate by taking care of water use efficiency and maintenance of photosynthetic ability. Thus alterations in transcriptome, proteome and metabolome during drought stress is essential for recovery of plant from stress and maintenance of its life cycle.

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