

Molecular Response of Plants to Drought, Cold and Heat Stress - A Review

Akula Dinesh^{1*}, Baramappanavara Muralidhara¹, Sunil Gangurde²
and More Yogeshwar³

¹Department of Genetics and Plant Breeding, University of Agricultural Sciences, Raichur, Karnataka, 584104, India.

²Department of Molecular Biology and Agricultural Biotechnology, SRF, Indian Institute of Millet Research, Hyderabad, 500030, India.

³Department of Plant Pathology, PDKV, Akola, Maharashtra, 444104, India.

Authors' contributions

This work was carried out in collaboration between all authors. Author AD designed the study, wrote the protocol, collected the literature, interpreted the data and prepared the initial draft. Author BM gathered the initial data and performed preliminary data analysis while authors SG and MY performed manuscript editing and review. All authors read and approved the final manuscript.

Article Information

DOI: 10.9734/ARRB/2016/26700

Editor(s):

- (1) Jin-Zhi Zhang, College of Horticulture and Forestry Science, Huazhong Agricultural University, China.
- (2) George Perry, Dean and Professor of Biology, University of Texas at San Antonio, USA.

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Complete Peer review History: <http://sciencedomain.org/review-history/15295>

Review Article

Received 29th April 2016
Accepted 13th June 2016
Published 7th July 2016

ABSTRACT

The increased abiotic stresses were severe threat to world food security paving to hunger death. To combat this situation crops with high tolerance should be developed. Crop improvement mainly depends on the improvement of traits that increase yield levels with high tolerance to abiotic stresses. It is known that the expression of the trait is purely under control of gene whose expression is temporal, spatial and stimulus specific. The molecular dissection of each tolerance mechanism at transcriptional, post transcriptional, translational and signaling pathway levels helps in easy understanding of the specific traits imparting tolerance. The identification of functional markers associated with abiotic stress tolerance and manipulation of key functional or regulatory genes

*Corresponding author: E-mail: dine.a32@gmail.com;

through molecular approaches like genetic engineering assist crop improvement with in short time. Hence, in this review we would summarize stimulus perception, signal transduction pathway (MAP kinase and ROS pathways), formation of regulatory protein, gene expression, synthesis of osmolytes (proline, glycine betaine, fructans) and other event that takes place under drought stress, heat stress and cold stress.

Keywords: Heat stress; drought stress; cold stress; gene expression; signal transduction.

1. INTRODUCTION

The rapid change in climate conditions increased the frequency of abiotic stresses like drought, high temperature, cold and floods which cause drastic reduction in productivity of crop [1]. The world population was predicted to rise by 31 million annually reaching up to 9.1 billion in 2050, becoming a major threat to food security [2]. It was estimated that there would be 70% high food requirement by 2050, imposing a greater task on plant breeder to develop high yielding cultivars that can withstand this huge demand. Among the abiotic stresses, water stress is recurrent and a key limiting factor for growth and development of crops [3]. In India, It was estimated that there would be a depletion of more than 40% of available water by 2025 leading to a drought stress for agriculture crops. For better understanding of stress, the definitions associated with different abiotic stresses are stated herein. Heat stress is defined as rise in temperatures usually 10-15°C above optimum conditions, which cause irreversible damage. Low-temperature stress includes chilling stress (<20°C) or freezing stress (<0°C), which cause crystallization of plasma membrane. The water stress is the situation, where a plant's water potential and turgor are decreased enough to inhibit normal plant function [4].

Unlike, experimental crop stand, the crops grown in natural condition experience unpredictable multiple stresses at single point of time which leads to huge yield loss. Maize grown at high temperature coupled with severe water stress during pollination result in yield loss up to 100 percent. This may be due to reduction in the quantity and quality of pollen produced, low pollen viability and silk receptivity [5-6]. In general, the reduction in crop yield depends on stress characteristics like duration of exposure, intensity of stress, combination of stresses and number of exposures. Under multiple stresses, maize crop showed 1.7% reduced yield compared to 1% yield reduction under sole heat stress [7]. In pigeon pea, moisture stress at pre-flowering stage resulted in photosynthesis

reduction by more than 50% [8]. Crop improvement for abiotic stress tolerance is a tedious and involves high end scientific knowledge to understand quantitative nature of the traits. Plants being sessile, has the capability to initiate molecular, physiological and morphological changes to any stress and act according to it [9]. Understanding molecular mechanisms and application of molecular approaches are of great significance to crop improvement. Through molecular approaches the genetic gain per unit time has been high compared to conventional basis. This led to an increased research activity to understand the system biology of different crops under abiotic stresses (Fig. 1) [10]. The present review is an attempt to document the pathways and crosstalks involved in response to different abiotic stresses and deals more about the changes that takes place at molecular level.

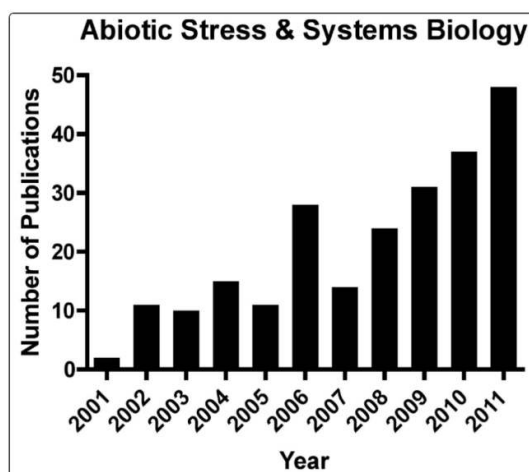


Fig. 1. Trends in research towards abiotic stresses

(Source: Cramer et al. 2011) [10]

2. SIGNAL TRANSDUCTION MODEL

The pathway of gene expression involves cascades of stimulus perception, signal transduction and target protein modification or

formation. Signal perception in plants is not well studied, but it was believed that plasma membrane is responsible for perceiving and transmitting signals to interior of the cell. The molecules like receptor-like kinases and G-protein in plasma membrane were mostly studied receptor molecules under abiotic stress to understand the signal perception and transmitting to signal transduction pathway [11]. Signal transduction involves interaction between spatial and temporal signaling molecules. The gene expression is specific to stimulus received by the receptor molecules present in the plasma membrane. A general signal transduction pathway involves 1) perception of stimulus 2) activation of signaling pathways 3) production of ROS/secondary messengers 4) activation of transcription factors 5) alter gene expression 6) synthesis of gene products/osmolytes. The secondary messengers adjust the calcium levels and activate protein phosphorylation. The phosphorylation of inactive proteins may directly involves in cellular protection by protein folding or expression of genes specific to stress [12]. The prominent plant signal transduction pathway involves mitogen activated protein kinase (MAPK) reactive oxygen species (ROS). All the signal transducing molecules are interconnected *i.e.* activation of one pathway leads to expression of another pathway.

3. MITOGEN ACTIVATED PROTEIN KINASE (MAPK)

Mitogen activated protein kinase was one of the most studied signaling pathways in plants under drought, cold and heat stress [13]. A typical MAPK cascade consist of least three protein kinases namely MAPKKK, MAPKK and MAPK, whose activation takes place in a sequential manner through protein phosphorylation (Fig. 2). An activated MAPKKK first activates MAPKK through phosphorylation of threonine residues located in the activation loop. Then the activated MAPKKs in turn activates following MAPK. The activated MAPK phosphorylates specific transcription factor, phospholipases, cytoskeletal proteins, which can lead the expression of genes in response to environmental stimuli.

4. REACTIVE OXYGEN SPECIES (ROS)

The cell organelles like chloroplasts, mitochondria and peroxisomes are the major

sites for ROS production in plant cells. Under abiotic stresses, mitochondria (electron transport), chloroplast (mehler reaction) and peroxisomes (glycolate oxidase reaction) are the three major contributors to ROS signalling [14]. The production of ROS molecules leads to oxidative stress which is injurious to plants, but over the course of evolution, plants developed scavenging mechanisms to overcome oxidative stress and maintaining sensitive levels of ROS molecules as signal transduction mediators for expression of corresponding genes [14]. The general ROS signal transduction involves sensing of reactive oxygen species by receptors molecules or heat shock transcription factors followed by activation of different transcription factor namely zinc finger proteins, WRKY transcription factors and MBF1c. The activated transcription factors binds to respective cis-acting element for gene expression. To maintain the continuity of gene expression, Rboh proteins helps in increasing the ROS signal necessary for gene amplification [15].

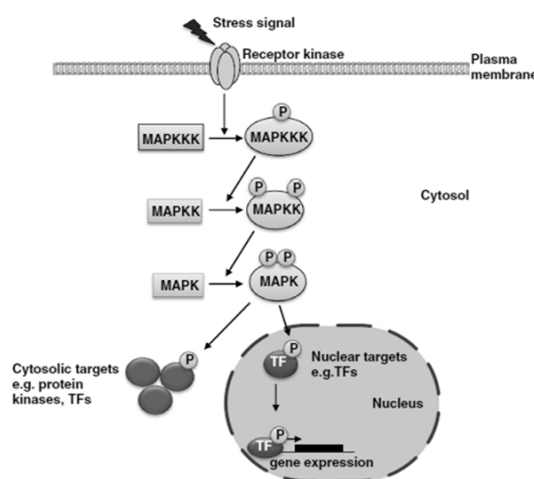


Fig. 2. A typical MAPK cascade pathway (Source: Danquah et al. 2013) [16]

5. MOLECULAR RESPONSE OF PLANTS TO DROUGHT STRESS

Abscisic acid (ABA) is a multifunctional phytohormone, which synthesizes storage proteins, promotes plant growth, development and adaptation to various abiotic stresses, particularly hydric stress [16]. The ABA is described as “stress hormone” because its accumulation controls the expression of stress-responsive genes. Upon sensitization of plant to

drought and salt stress, the calcium dependent signal transduction pathway comes into role and activates transcription factors through protein phosphorylation. The activated transcription factor encodes zeaxanthin oxidase enzyme which leads to epoxidation of zeaxanthin to violaxanthin which later forms neoxanthin. The so formed neoxanthin is converted to xanthoxin under the influence of enzyme 9-cis-epoxycarotenoid dioxygenase enzyme (NCED). Finally, the ABA is produced from xanthoxin via ABA-aldehyde. The enzyme ABA-aldehyde oxidase (AAO) and molybdenum cofactor sulfurase (MCSU) catalyses ABA-aldehyde to Abscisic acid. Once the ABA is synthesized, rhythmically ABA dependent downstream genes starts expressing. The gene expression involves interaction between three protein classes (1) regulatory component of ABA receptor (RCARs) (2) SNF1-related protein kinase 2 (SnRKs) which are positive regulators and (3) Protein Phosphatase 2Cs (PP2Cs) which act as negative regulator [17]. The interaction of above three protein classes leads to expression of corresponding genes. In presence of ABA, the RCAR binds to PP2C complex and deactivates PP2C function, thus allowing activation of SnRKs which leads to expression of transcription factors, activation of ion channels, folding of target proteins and expression of ABA-responsive genes (Fig. 3). On contrary, plants sensitive to drought stress fails to accumulate of ABA hormone, under such conditions the PP2Cs dephosphorylates SnRK2 protein. The dephosphorylated SnRK2 does not lead to expression of genes that confer tolerance. Under this situation, plant behaves abnormal due to inability to form proteins and ion channels which combat the stress. The protein products of the drought-inducible genes were categorized into two groups viz. functional proteins and regulatory proteins. The functional proteins directly involved in tolerance mechanism which includes molecular chaperones for protein stability, late embryogenesis abundant proteins which promote desiccation tolerance, enzymes for osmolyte synthesis to maintain cell turgidity and water potential, water channel proteins and detoxification enzymes to scavenge ROS toxicity etc., . The regulatory proteins involves in gene regulation by controlling signal transduction, amplification of signaling molecules like ROS, calmodulin-binding protein, activation of transcription factors, protein kinases, protein phosphatases etc. upon retrieval of stress the abscisic acid would degrade to form phaseic acid [18].

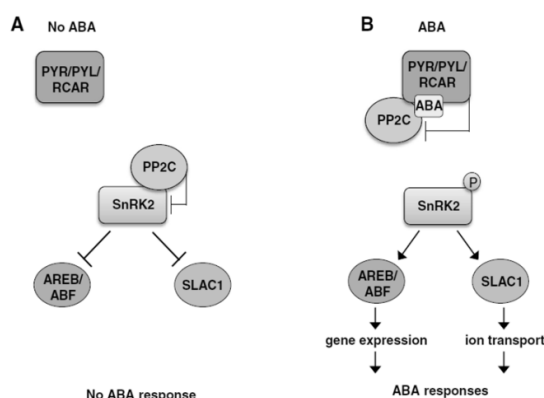


Fig. 3. ABA dependant signal transduction and expression of genes.

(Source: Danquah et al. 2013) [16]

6. MOLECULAR BASIS OF STOMATAL CLOSURE UNDER STRESS

In course of evolutionary stress, the plants have developed ability to close their stomata and thereby reducing the water loss for substantial growth. At physiological level, drought tolerance is accomplished by closure of guard cell due to accumulation of solute particles. The dramatic opening and closure of stomata is under the control of fluctuating ions, signal transduction pathway, SnRK2E/OST1, SLAC1 and KAT1 proteins. As stated above, the activation of SnRK2E/OST1 (open stomata 1) leads to expression of downstream genes responsible for stomatal closure. In one of the pathways, the activated SnRK2E/OST1 leads to phosphorylation of SLAC1 protein (slow anion channel-associated 1) which in turn mediates the efflux of Cl^- and malate^{2-} from guard cell. Simultaneously, SnRK2E/OST1 also prevents the inward flow of K^+ ions into the guard cell by inhibiting KAT1 protein [19]. Under these changes, the stomatal apparatus becomes closed and retaining the water loss and promotes the increased water uptake. Once the stress has removed, SnRK2E/OST1 becomes inactive and favors inward flow of K^+ ions into guard cells. The loss of function of KAT1 protein revealed its role in stomatal opening [20]. Stomatal closure can also be induced by calcium-dependent ABA pathway. Under this pathway, CPK21, CPK23 and OST1 are two positive regulators of stomatal closure. Finally the synthesized ABA will be transported to other cells, mediated by ATP-binding cassette (ABC) transporters embedded in plasma membrane.

7. MOLECULAR RESPONSE OF PLANTS TO COLD STRESS

In plants, cytoskeleton act as sensory machine for low temperature stress [21]. This sensory machine leads to increased Ca^{2+} levels in the cytoplasm, which act as second messenger for signal transduction to the stress inducible gene. The CBF genes (C-repeat-binding factor) control major share of the low temperature induced genes [22]. The elevated Ca^{2+} levels in the cell leads to activation of ICE transcription factors (inducer of CBF expression) which binds to cis acting element called as inducer of CBF expression region (ICER) which inturn leads to the expression of CBF transcription factors. This group of transcription factors binds to CRT (C-repeat) cis-acting element located in upstream of the many cold inducible genes. It was found that CBF genes alone can regulate about 12% of the cold response. The CBF genes primarily includes three genes CBF1, CBF2 and CBF3. Among the three genes, it was reported that the knock out mutants of *cbf2* gene showed overexpression of CBF1 and CBF3 and leading to increased freeze tolerance. In *Arabidopsis*, the over expression of CBF1 genes enhanced the CBF proteins and increased the tolerance to low temperature [23].

8. MOLECULAR RESPONSE OF PLANTS TO HEAT STRESS

Rise in temperatures leads to early induction of heat stress factors (Hsf) and heat shock proteins (HSP) which are considered to be key players imparting thermo-tolerance to plants. [24]. The increased temperature leads to oxidative stress in plants, producing ROS complex which functions as signaling media. The accumulated ROS is sensed by histidine kinases, which binds to monomeric heat shock factors (HsfA4a). This binding allows the movement of heat shock factors from cytoplasm into the nucleus. In the nucleus, monomer HSF form in to active trimers, under this this situation, the HSF will bind to the heat shock element present in the promoter region of the respective heat induced genes. Simultaneously, the MAPK signaling pathway leads to expression of different transcription factors, respiratory burst oxidase homologs (Rboh) and multiprotein bridging factor 1 (MBF1). The heat induced transcription factors viz. Zat and WRKY families leads to expression of stress responsive antioxidant enzymes, which scavenge the toxic ROS molecules. The MBF1c acts as a transcriptional co-activator for stress

responsive genes. The Rboh plays an important role in maintaining the ROS molecules at a safer level such that the ROS signal pathway continues until the stress is withdrawn [25]. The production of functional heat shock proteins depends on the successful transcription and protein folding responsible for heat stress tolerance [26].

9. ROLE OF OSMOLYTES UNDER DROUGHT, COLD AND HEAT STRESS

The water soluble low molecular weight compounds known as osmolytes are one of the strategies to face the stress situation. The most important solutes particles produced by plants include proline, glycine betaine, sugars (mannitol, sorbitol and trehalose), polyols and polyamines [27]. Among the above stated osmolytes, proline is most extensively studied amino acid which gets accumulated under drought, salinity, and oxidative stress and in response to different abiotic stresses [28]. For the first time, the osmoprotective function of proline was discovered in bacteria under high salinity. The study revealed that a casual association between proline accumulation and salt tolerance was observed.

10. PROLINE SYNTHESIS AND DEGRADATION

In plants, reduction of glutamate leads to synthesis of proline. Under stress, the signal transduction pathway leads to activation of transcription factors which binds to two genes, whose protein product will combine to form the enzyme pyrroline-5-carboxylate synthetase (P5CS). The P5CS reduces glutamic acid to glutamate-semialdehyde (GSA) and simultaneously converted to pyrroline-5-carboxylate (P5C) [29]. The P5C later reduces to proline under action of P5C reductase enzyme, a protein product of single gene (P5CR). Once the favorable condition has set in, the catabolism of proline take place in mitochondria. The alternate pathway for proline synthesis involves ornithine metabolism. The cascade includes in transamination of ornithine to glutamate-semialdehyde then to pyrroline-5-carboxylate by the action of ornithine-delta-aminotransferase [30]. Proline being a multifunctional amino acid, works as molecular chaperone, maintains balanced redox potential of the cell, regulate programmed cell death, protects and stabilizes ROS scavenging enzymes [28,31].

Some group of plant species synthesizes trehalose as osmolyte which prevents protein degradation and aggregation under stress [32]. Under freezing temperatures, high water soluble solutes called fructans were essentially synthesized which prevents the crystallization of plant cells [33]. Under abiotic stresses, salicylic acid regulates proline and glycine betaine metabolism, photosynthesis and production of antioxidants [34-36]. Moreover, salicylic acid concentration in plant cells is of great importance as like ROS molecules. The lower concentration of applied salicylic acid imparts tolerance to abiotic stresses and *vice versa*. Plants having desired levels of glycine betaine naturally show improved resistance to drought and saline stress [37]. The polyamine accumulation in plant cell reports positive correlation with stress tolerance [38-39].

11. CONCLUSION

In the present scenario, field crops encounter multiple abiotic stresses. The crop improvement for such multiple stresses would be a boon for the farmers. The plant molecular breeding based on the development of molecular markers, candidate gene identification or gene expression profiles and transgenic approaches is frequently utilized to enhance the efficiency of conventional breeding. Hence, understanding the molecular changes at genetic level and tracing different crosstalks common among multiple stresses using molecular approaches would be promising. Currently, the progress is confined to identification and validation of genes that can improve stress tolerance of crops. But, the integration of multiple omics studies with system biology approach would help in tracing new areas of interactions and regulation that control the stress tolerance.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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