



Signaling for Abiotic Stress Tolerance in Plants: A Review

Mandeep Singh¹, Usha Nara¹, Antul Kumar², Chandan Jaswal¹

10.18805/ag.R-2306

ABSTRACT

Plants copiously rely on intense sensitivity recognition and acclimation mechanisms to cope against various environmental perturbations. Abiotic stresses such as water availability (drought or flooding), salinity, nutrient stress and metal stress are grievous threats to the global agriculture as they hinder the crop plant to attain its whole genetic potential resulting in the notable yield loss. Signal transduction networks validate the plants in stress signal perception accompanied by transduction than finally inception of the response. Stress signal transduction and its perception is a hugely decisive step to conquer these environmental obstacles for the better growth and survival of the crop plant. This review emphasizes on various pathways namely hormone signaling and their cross talk, ROS signaling, ABA signaling, Ion homeostasis, MAPK pathways, SOS signaling and transcriptional factors (TFs). Peculiarly, in future recent biotechnological innovations will help in understanding the gene function and ingress to whole genome sequences provide new guidance for crop refinement.

Key words: Abiotic stress, Crop improvement, Crop, MAPK, Signaling cascade.

Abbreviations: ABA: Absciscic acid; CDPK: Calcium-dependent protein Kinase; JA: Jasmonic acid; MAPK: Mitogen-activated protein kinase; ROS: Reactive oxygen species; SOS: Salt overly sensitive; TFs: Transcription factors.

Abiotic stress in crop plants acts as a great yield-restricting aspect (Canter 2018; Zorb *et al.* 2019). Plants already flourishing in adverse conditions can cope up from the abiotic and biotic stresses by managing their tone to environment (Bailey-Serres *et al.* 2019; Hu *et al.* 2022). Plants reproduce and grow in a vigorous environment able to see instantaneous transformation in conditions like temperature, intensity of light or interaction with some biotic factors. Due to sessile nature of the plants, the devastating effect of climate results in the alleviation in the growth of plant (Zhu 2016). Changing environment conditions include various types of abiotic stress namely, cold, heat, excess of salt, nutrient deficiency, or some noxious metals such as cadmium, arsenate and aluminium in the soil. Out of these abiotic stress, salt, drought and stress of temperature are the main factors which affect the agricultural productivity (Fedoroff *et al.* 2010; Vaughan *et al.* 2018; Waqas *et al.* 2017; Zafar *et al.* 2018; Singh *et al.* 2021a). Among abiotic stresses, drought and salinity has been reported to adversely affect >10% cultivable land leading to decrease in crop productivity up to 50% (Roychoudhury *et al.* 2013). Plants adapt various mechanisms to escape itself from various environmental injuries like biotic and abiotic stresses. In, escaping itself from stresses, stress signals perception and transduction of signals is an influential step for various responses to manage the stress whether there is a loss in yield as well as growth of the plant or for the survival of the plants (Bailey-Serres *et al.* 2019; Bobade *et al.* 2021).

Steps in signaling pathways

First step in signaling pathway is performed by the molecular sensors or receptors such as hormones, phytochromes, receptor-like kinases etc. Second step includes the inception of secondary signaling molecules like ROS (reactive oxygen species), inositol phosphatase and abscisic acid. Third step

¹Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana-141 004, Punjab, India.

²Department of Botany, Punjab Agricultural University, Ludhiana-141 004, Punjab, India.

Corresponding Author: Mandeep Singh, Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana-141 004, Punjab, India. Email: mandeepsingh91483@gmail.com

How to cite this article: Singh, M., Nara, U., Kumar, A. and Jaswal, C. (2022). Signaling for Abiotic Stress Tolerance in Plants: A Review. *Agricultural Reviews*. DOI: 10.18805/ag.R-2306.

Submitted: 17-06-2021 **Accepted:** 07-04-2022 **Online:** 23-05-2022

in signaling pathways is through the secondary signaling molecule-mediated pathways including the intonation of Ca^{2+} level which cause the inception of protein phosphorylation cascades i.e., MAPK, MAPKK, MAPKKK, CDPK and SOS1, SOS2, SOS3 and transcription factors. General diagrammatic representation of the plant signal transduction pathway against abiotic stresses is shown in the Fig 1.

Hormones and their cross talk in signaling

ABA already showed its potential role in abiotic stress via signaling but other hormones also play a crucial role in the signaling of plants under various abiotic stresses is discussed below.

Jasmonic acid (JA) plays an important role in abiotic stress signaling. Activation of jasmonate biosynthesis occurs whenever there is a stress condition in the plant (Wasternack 2007) and several genes are managed as a result of drought stress which take part in JA signaling (Huang *et al.* 2008). The change in JA level in the plants has also been reported (Choudhury *et al.* 2018). External application of methyl JA

(MeJA) or Jasmonic acid leads to its conversion into bioactive form, namely iso-Jasmonyl-L-isoleucine (JA-Ile). This bioactive form of JA binds with the ^{SCF}COI (coronatine insensitive) complex (Sheard *et al.* 2010). Munemasa *et al.* 2007 and Suhita *et al.* 2003, 2004 reported the crucial role of JA in the closing of stomata during drought stress. The anion channels (S-type) were activated by MeJA, with the help of which CDPK was activated leading to the stomatal closing during drought conditions (Munemasa *et al.* 2007). Zhou *et al.* 2019 observed the production of jasmonic acid within seconds after wounding suggesting that endogenous hormonal regulation in the primary stress response.

Ethylene biosynthesis tends to increase during drought condition. Ethylene synthesis has been induced by increasing the synthesis of enzymes namely 1-Aminocyclopropane-1-carboxylic acid (ACC) oxidase and ACC synthase. Ethylene promotes plant senescence which helps the plant to decrease water losses during stress. Ethylene encourages adventitious root emergence helping the plant to grow via uptake of water during flooding conditions (Pistelli *et al.* 2012; Sairam *et al.* 2008). Inhibition of stomatal closing has been reported in *Arabidopsis* plants on exposure to external application of gaseous ethylene (Tanaka *et al.* 2005). Accumulation of ABA is negatively correlated with the ethylene production resulting in increased concentration of ABA (Absciscic acid) with the decrease in concentration of ethylene during the water stress conditions.

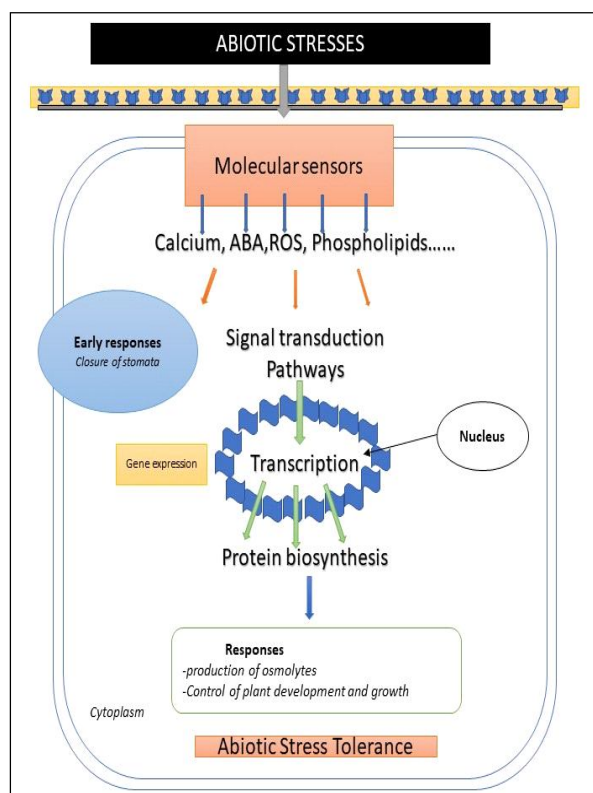


Fig 1: Schematic depiction of signal transduction pathways in response to various abiotic stresses such as temperature, drought and salinity.

Brassinosteroid (BR) is a phytohormone having crucial role in the development and growth of the plant and acts as a defense against various abiotic and biotic stresses. BR in cooperation with ABA helps in the stomatal closing to reduce water losses via transpiration. Similar study in *Vicia faba* showed the stomatal closing by the epibrassinolide (EBL) application (Haubrick *et al.* 2006). External application of epibrassinolide (EBL) in *Brassica napus* and *Arabidopsis thaliana*, which are water scarcity resistance, causes resistance against drought (Fariduddin *et al.* 2014). BRs have interaction with other hormones to induce the tolerance against abiotic stresses. BR in plants decrease the synthesis of stress inducing hormones such as IAA (Indole acetic acid) and ABA but amount of cytokinin remained unchanged (Avalbaev *et al.* 2010).

Auxin, a phytohormone, helps in controlling the H⁺-ATPase movements in the guard cells. The invasion of K⁺ ion from the guard cells was promoted when there is an emission of H⁺ ion from the guard cells. Auxin when present in high amount, give rise to emission of K⁺ and inhibit the invasion resulting in closing of stomata but in low concentration of auxin, there is removal of K⁺ ion leads to stomatal opening (Daszkowska-Golec and Szarejko 2013). ARFs (auxin response factors), Aux/IAAs (auxin/indole-acetic acid) and TPSs (TOPELESS proteins) are the three main transcription regulators which manage the auxin response genes transcription (Causier *et al.* 2012; Szemenyei *et al.* 2008; Zouine *et al.* 2014). Out of these three protein families, it is found that ARF family has its role in regulating the expression of genes. Many OsARFs are there in rice which play role in response to drought and salt stress (Jain and Khurana 2009). Cytokinin (CKs) restrict the stomatal closing and assigned in relation with ABA (Tanaka *et al.* 2006) Fig 2.

ROS signaling

Abiotic stresses, such as cold, drought and salt stress induce the ROS (Reactive oxygen species) accumulation namely hydroxyl radicals, hydrogen peroxide and superoxide. ROS induce signals and act as harming agents which cause stress injury to the cells. It is reported that H₂O₂ production was induced by presence of ABA (Guan *et al.* 2000). The production of ROS may be induced through various mechanisms in response to heat and light stress (Pospisil 2016). ROS may act as intermediate signals for closing of stomata (Zhang *et al.* 2001), Ca²⁺ channels activation in guard cells and biosynthesis of ABA (Zhao *et al.* 2001). ROS are produced continuously as products of metabolic pathways in the different sections of the cell. ROS are produced in the course of aerobic photosynthesis and photorespiration (Kotchoni *et al.* 2006). Increase in the ROS molecules can be seen in peroxisomes under various type of abiotic stresses (Mittler 2002). It acts as intracellular signaling molecule and various investigations shows that transgenic plants having high rate of ROS generation and high ROS-scavenging capacity indicate much tolerance against stress (Hasegawa *et al.* 2000; Kocsy *et al.* 2001).

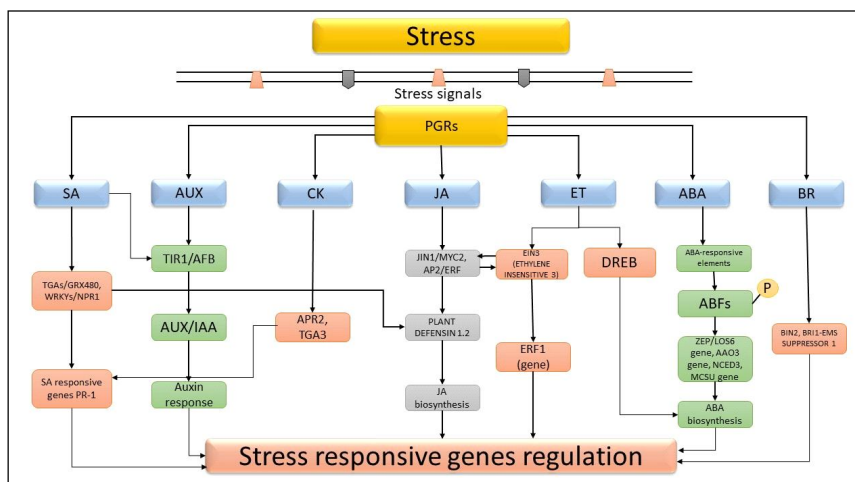


Fig 2: Signaling of plant growth regulators and their crosstalk.

Possessing the property of most energetic compound and high reactivity ROS molecules are suitable in activation of plant stress signaling (Foyer and Noctor 2005). A study on yeast and animal suggests that MAPK pathway which was activated by histidine kinase also play a role in mediating the ROS signaling (Xiong and Zhu 2002). It has been reported that ROS has a role in gene activation of peroxy and alkoxy radicals and lipid peroxidation products Spiteller *et al* 2001. O_2^- and H_2O_2 play a role in signaling that causes variation in the transcript level of Cu/Zn-SOD in *Pisum sativum* (Pea) under cadmium (Cd) stress (Romero-Puertas *et al.* 2004). ROS has a role in signaling for acclimation against chilling stress and photo-oxidative stress. Yang *et al.* 2009 reported the involvement of H_2O_2 in signaling backed up by its role in infection of proline level. The pre-treatment of H_2O_2 was reported to enhance the non-enzymatic and enzymatic antioxidants in four species of *Digitalis* namely *D. cariensis*, *D. davisiana*, *D. trojana* and *D. lamarckii* (Cingoz *et al.* 2014).

ABA signaling

Abiotic stresses such as drought and salt stress increase ABA gathering and on external ABA application, plants undergo certain stresses like osmotic stress. To know whether some or all the response of osmotic stress are of ABA dependent, mutants of Arabidopsis such as *abi1*, *abi2* and *aba1* and *aba2* have been used. Many studies on stress responsive genes showed that some genes are completely ABA dependent while some are completely ABA independent and some others are partially dependent on ABA (Sah *et al.* 2016, Vishwakarma *et al.* 2017). The independent and dependent gene regulation of ABA regulated by RD291 gene acts as a superior model. The accumulation of RD29A transcript is partially blocked by *abi1* and *aba1* as shown by several studies on osmotic stress induction which encourage independent and dependent regulation of ABA. DRE (dehydration responsive element) element sequence in the RD29A gene promoter has been identified by scientist revealing its necessity for induction of osmotic stress.

Normally DRE elements cannot be activated by ABA but osmotic stress activated DRE requires ABA, for its activation. ABA role in response to cold stress is still unclear but ABA is believed to have an important role in response to cold. It was reported that there is a temporary accumulation of ABA in response to cold, other studies showed a tiny accumulation of ABA in response to cold. Many studies results showed the external application of ABA to the plant confer tolerance in plants against cold stress Fig 3.

ABA-Independent pathways

DREB are the transcription factors that help in inducing genes which are stress-related and provide resistance against various abiotic stresses. DREB1 and DREB2 are the two main group of DREB. Low temperature stress involves DREB1 while dehydration involve DREB2. They come under ERF (ethylene responsive element binding factors) family of transcriptional factors. A preserved 58-59 amino acid region (ERF region) has been shared by the ERF proteins and these regions attach to *cis*-element which are found in several PR (pathogen related) gene promoters that involve in ethylene response and these regions attach to the DRE (dehydration responsive element) pattern which involve in the dehydration responsive genes (Agarwal *et al.* 2006). DREB proteins of TFs (transcriptional factors) contains an ERF/AP2DNA-attaching region. The amino acid sequence showed resemblance in the c-terminal acidic region and also at the N-terminal region in nuclear localization signal (Agarwal *et al.* 2006). ERF /AP2DNA-attaching region are found extensively in plants such as maize, rice, tobacco, tomato and Arabidopsis.

ABA-Dependent pathways

Regulatory protein kinases play an important role in phosphorylation of targets (downstream) which initiate the transcriptional events (Furihata *et al.* 2006; Johnson *et al.* 2002; Umezawa *et al.* 2009). ABA-dependent pathway of signaling depends upon the MYB/MYC transcription family (Abe *et al.* 2003). ABA regulated 15 genes have been

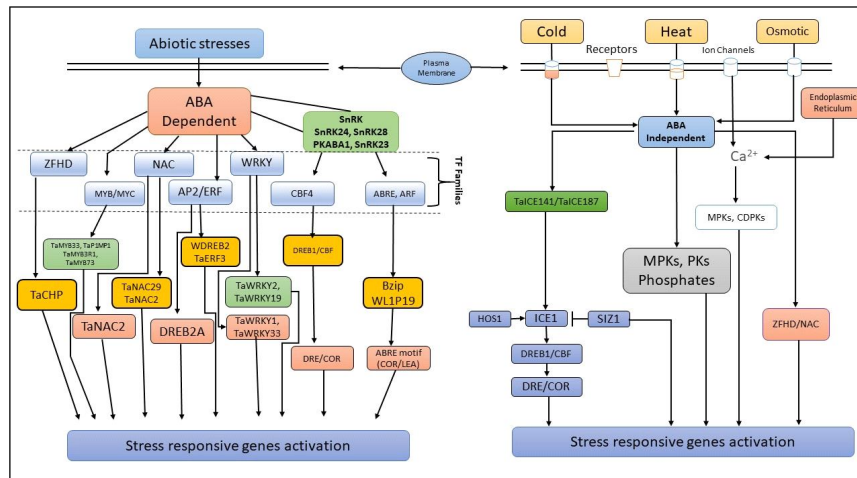


Fig 3: ABA-independent signaling in response to osmotic, heat, cold stress and ABA-dependent signaling channel in response to temperature stress.

identified, out of which 9 are induced whereas 6 are repressed (Zhang *et al.* 2012b). It is also reported that out of these 15 genes, 14 genes respond to the osmotic stress which is caused by PEG (Zhang *et al.* 2012b). Genes TaMYB33 and TaMYB32 helps in the salt tolerance and these genes were overexpressed in the Arabidopsis plant under salt stress (Qin *et al.* 2012; Zhang *et al.* 2012a). TaMYB33 also play a major role in the production of antioxidants to detoxify the damaging ROS (Reactive oxygen species) (Qin *et al.* 2012). External application of salicylic acid and ABA help in the induction of TaPIMP1 MYB and this MYB protein act as a mediator for responses in different type of hormones or acts as an integral point of salicylic and ABA signaling (Zhang *et al.* 2012a). Some members of the family MYB, namely TaMYB3R1, found to be play an important role in hormonal signaling.

Another family of protein is WRKY-type family of transcription factors have an important role in the ABA-regulated pathway in abiotic stress signaling. A study on this family shows that there are 40 members in this family. TaWRK19 and TaWRKY2 were the two which are characterized in wheat crop and both were induced through various abiotic stresses. TaWRKY19 enhances cold, drought and salt tolerance led by its overexpression (Niu *et al.* 2012).

Ion Homeostasis (Sodium and Calcium)

There is the propensity of a cell or an entity to regulate its internal stable state in response to different types of environmental disturbance. Hypersaline environment cause disturbance of stable ionic state of Cl^- and NaCl in addition to Ca^{2+} and K^+ . Presence of high amount of sodium (Na^+) in the environment has great agricultural importance because saline solutions impose stresses on the plants. Uptake of K^+ ion by cells of root found to be disturbed by Na^+ ions (Hasegawa *et al.* 2000). Cell membranes receptor sense the amount of Na^+ present externally whereas Na^+ -sensitive cytoplasmic enzyme or membrane proteins perceive the Na^+ present internally (Turkan and Demiral 2009). Accumulation

of excess of Na^+ in leaf cells cause toxicity in the production of enzymes (Hasegawa *et al.* 2000). Presence of high amount of Na^+ causes necrosis in the older leaves, which reduce the life span of leaves, resulting in the low productivity (Munns 2002). Compartmentation of Na^+ ions in vacuole decrease the amount of sodium ions in cytoplasm. Presence of membrane transporters in wide range support the plants to fight against external stresses (Maser *et al.* 2002). *Arabidopsis* was the first plant in which the cation exchanger (Na^+/H^+) was found.

MAPKINASES stress signaling

The plant MAPK substrate identification is mandatory to understand the mechanism and function of MAPK. Several scientists reported around 700 putative MAPK substrates through targeted experiments and by using the novel approaches such as protein array screening and phosphoproteomics (Hoehenwarter *et al.* 2013; Rayapuram *et al.* 2018). MAPK pathways are the signaling component that are used to transduce cellular signals in the cell (Morrison, 2012). These MAPKs are initialized by phosphorylation (dual) of threonine and tyrosine remnants in a partially unorganized part of the catalytic domain. Threonine remnant phosphorylation guide the hydrogen bond formation on the MAPK surface by joining the amino-terminal with the unorganized part. Tyrosine remnant phosphorylation guide to the formation of new H-bond and refolding of unorganized part to make a structure (Rodriguez Limardo *et al.* 2011). The JNK and p38 families of MAPK are initialized by the intra and extracellular stress to the cell (Cuadrado and Nebreda 2010; Davis 2000).

The phosphorylation of MAPK act as connection between the transcription factors (downstream) and the receptor (Upstream). These MAP Kinases are activated during the various abiotic stresses. MAPK cascade is composed of three protein kinase, which are linked with each other in their function, namely MAPK, MAPKK and MAPKKK (Agarwal *et al.* 2003). In MAPK cascade firstly MAPK

phosphorylate which initiate the specific MAPKK which upon phosphorylation give rise to activation of MAPKKK. This MAPK (activated) moves downstream in to nucleus, phosphorylates and activates the transcriptional factors which give rise to cellular response (Xiong and Yang 2003).

The p38 of MAPK family encodes four genes which are divided into two main subgroups namely p38 γ/δ and p38 α/β (Cuadrado and Nebreda 2010; Cuenda and Rousseau 2007). The JNKs of MAPK family coding three genes namely JNK3, JNK2 and JNK 1 which upon splicing give rise to 10 different types of isoforms. Out of these three genes, two genes JNK2 and JNK1 are expressed pervasively but the JNK3 gene expressed firstly in the brain (Davis, 2000). Isoforms of different type of MAPKK initiate specific MAPKs: MKK1 initialize ERK1, MKK2 initialize ERK2, MKK3 initialize p38 whereas MKK4 initialize p38 and JNK, MKK6 and MKK7 initialize p38 and JNK respectively. The MLK (mixed-lineage protein kinase) class of MAPKKs are initialized by Cdc43 and Rac1 which are the part of Rho GTPase family (Gallo and Johnson 2002). ATM (ataxia telangiectasia-mutated) protein kinase activates the stress-activated MAPKs in response when there is damage of DNA (Rhind and Russell 2012). Stress-activated MAPK play an important role in cellular pathology and physiology (Cuadrado and Nebreda 2010; Davis 2000). It plays a role in some particular examples like inflammatory stress, cell death and metabolic stress.

Cells when exposed to cytokines such as IL1 and TNF results in the stress-activated MAPKs activation (Lim and Staudt, 2013; Newton and Dixit, 2012). This pathway of activation needs TAB3 and TAB2 (ubiquitin-binding supplement protein) and TAK1 (isoform of MAPKKK). The TAK1 isoform is activated by the TAB proteins jointly with the K63-linked polyubiquitin chains (Chen, 2012). The IL1 receptor create autoubiquitylation (K-63 linked) of E3 ligase TRAF6 and receptor of TNF create ubiquitylation (K63-linked) of TRAF2/5 and RIP1 by E3 ligases cIAP1/2 (Lim and Staudt, 2013; Newton and Dixit, 2012).

Salt overly sensitive (SOS) signaling

Salinity tolerance in plants include the activation of signaling pathways namely salt overly sensitive (SOS) signaling (Ji *et al.* 2013). To alleviate the effect of various abiotic stresses, different pathways of signaling have been reported but none of them were perceive in proteins signaling terms. The results obtained from molecular, biochemical and genetic analysis were found to be different from the SOS pathway which makes the SOS pathway an exceptional pathway (Zhu 2001). Salt-elicited calcium signal is sensed by a myristoylated calcium-binding protein and then convert it for the downstream responses. SOS1, which is a salt tolerance effector gene, was regulated by SOS3 and SOS2. The transport activity of SOS1 was activated with the help of SOS3 and SOS2 (Qui *et al.* 2001). SOS genes are found to co-express itself and have a role in response to salinity stress in *Arabidopsis* plant (Ma *et al.* 2014). A study on the plasma membrane Na^+/H^+ exchanger in rice crop reveals

that the SOS1 gene have a significant role in adaptive response to salinity stress (El Mahi *et al.* 2019). SOS2 belong to a PKS family of proteins which is found only in plants (Guo *et al.* 2001). SOS2 contains two domains namely unique regulatory domain and SNF1-like catalytic domain which interact with SOS3. The domains of SOS2 interacts with each other for keeping the kinase inactivated. Attaching of regulatory domain with the SOS3 appears to damage the SOS2 intramolecular interactions which leads to opening of catalytic site (Guo *et al.* 2001).

SOS3 belongs to new subfamily of calcium binding proteins. These proteins are very similar with type 2B protein phosphatase (B-subunit of calcineurin) (Guo *et al.* 2001). It is also found that some of the SOS3 proteins in plant cells are not related with membranes as they are compatible with the nonmembrane-bound protein which target the SOS2-SOS3 complex (Ishitanim *et al.* 2000).

Transcription factors (TFs) in abiotic stress signaling

Transcription factors (TFs) are major regulators controlling the expression of gene and have a crucial role in development of plant, cell signaling, response to stress and cell cycling (Gonzalez *et al.* 2016). The pathways of signal transduction carry signal of stress to the end point of stress responsive expression of gene of signal transduction pathway. The pathway contains various cis-acting elements as well as transcription factors which are having a role in response to stress. There are two methods to improve the plants efficiency to withstand against various stresses. First managing the process of ion transport and reorganizing of the primary metabolism. Secondly changing and regulating the pathways of signaling. Out of these two second approach is more helpful because signaling components such as translational and transcriptional consist regulatory factors (Golldack *et al.* 2011; Singh *et al.* 2021b, c). Several TFs have been investigated which gave response to stresses with the help of molecular tools such as transcriptomics, functional genomics and proteomics in several crops including sugarcane (Mustafa *et al.* 2018). Transcription factors have been classified into two classes in response to drought stress and these are ABA dependent and ABA independent transcription factors (Gujjar *et al.* 2014).

DREB family of transcription factors are having an important role in response to various abiotic stresses (Gutha and Reddy 2008). They are found to help in the activation of genes such as *cro15A* and *rd29A* which helps the transgenic plants to withstand against high salinity and drought conditions. DREB TFs have been classified into two classes namely DREB1 and DREB2. DREB1 have been involved under low temperature while DREB2 has been involved under dehydration in the signal transduction pathway (Agarwal *et al.* 2006). It has been reported that DREB2A and DREB2B are the analogous TFs which act as stress responsive genes.

bZIP (basic leucine zipper) proteins have a bZIP domain having 40-80 amino acids preserved domain consisting two

Table 1: A number of WRKY TFs identified in plant species.

Crop	Scientific name	Plant Type	WRKY Genes	References
Barley	<i>Hordeum vulgare</i>	Monocot plant	126	Uluhan <i>et al.</i> 2019
Arabidopsis	<i>Arabidopsis thaliana</i>	Dicot plant	90	Bao <i>et al.</i> 2018
Sugarcane	<i>Saccharum spontaneum</i>	Monocot plant	39	Li <i>et al.</i> 2020
Rice	<i>Oryza sativa</i>	Monocot plant	128	Lilly and Subramanian 2019
Physic nut	<i>Jatropha curcas</i>	Dicot Plant	61	Xiong <i>et al.</i> 2013
Maize	<i>Zea mays</i>	Monocot plant	161	Wang <i>et al.</i> 2018
Wheat	<i>Triticum aestivum</i>	Monocot plant	171	Li <i>et al.</i> 2019a
Cotton	<i>Gossypium hirsutum</i>	Monocot plant	238	Gu <i>et al.</i> 2018

structures, one, the region for the attachment of transcription factors and the other needed for the dimerization of TFs called as leucine zipper (Nijhawan *et al.* 2008). The bZIP family of TFs helps in the regulation of various mechanisms such as tissue differentiation, seed storage protein gene regulation, osmotic control, energy metabolism, pathogen defense, sugar and hormone signaling, light response, unfolded protein response and cell regulation (Nijhawan *et al.* 2008). It has been reported that the bZIP proteins have a crucial role in response to salinity stress (Das *et al.* 2019; Liang *et al.* 2016; Liu *et al.* 2014; Zhu *et al.* 2018).

MYB family of TFs has an important role in mechanism of biotic and abiotic stress, development and metabolism. Among all R2R3-MYB family is the largest family of MYB which is present in the plants (Dubos *et al.* 2010; Millard *et al.* 2019; Li *et al.* 2019b). Many genes have been identified from MYB family (Zhang *et al.* 2012).

WRKY family of transcription factors have WRKYGQK sequences which bind with W-BOX (TTGAC) at the promoter. WRKY family have large number of transcription factors which are indicated by the presence of chain of 60 amino acids (Shimono *et al.* 2007). This family is the large family of transcription factors composed of 90 members in rice and 74 members in arabidopsis (Eulgem and Somssich 2007; Ulker and Somssich 2004). The WRKY proteins are divided into three groups on the basis of zinc finger motifs and WRKY domain numbers (Ulker and Somssich 2004). WRKY alone can't associate in stress like other MYB and AP2-EREBPs, but this WRKYs are expressed when they are in combination *i.e.*, biotic as well as abiotic stress (Bai *et al.* 2018). A number of WRKY family TFs have been identified in several plant species as shown in the Table 1.

NAC transcription factors have important role in salinity stress. This family of TFs contains domain such as NAM (no apical meristem), CUC2 (cup-shaped cotyledon) and ATAF1-2. Arabidopsis has 106 whereas rice has 149 NAC family transcription factors (Gong *et al.* 2004; Xiong *et al.* 2005). The domain of NAC consists of 150-160 residues and classified in to five subdomains *i.e.* A to E (Ooka *et al.* 2003). It is also reported that these NAC transcription factors also play a role in controlling the various processes such as flowering, biotic stress, anther dehiscence, abiotic stress and lateral root development (Gujjar *et al.* 2014). *CaNAC064*, which is a NAC transcription factor was reported to have a

capability to resist the cold stress when they interact with haplo-protein which were induced during low temperature conditions (Hou *et al.* 2020). Over expression of *EcNAC67* TF in transgenic rice exhibit lower spikelet sterility, higher seedling vigour and increased performance in tolerance to stress caused by drought (Rahman *et al.* 2016).

FUTURE PROSPECTS

Signaling pathways and the cross-talk between several pathways plays a very impressive role in plant abiotic stress responses. Stress responsive genes involvement in several metabolic approaches to emphasize the tolerance against stress in plants has common implications. More efforts are still essential to know much about the outcome of each gene which is persuaded by ABA and its association arrangement to recognize the complexity of salinity stress pathways of signaling. We still need to know about the different types of ABA-responsive genes. As the new powerful appliance *viz.*, proteomics, genomics and transcriptomics are appearing, understanding these signaling will improve and provide pathways to tolerate various stresses. Genetic engineering now a days play a crucial role in signal study but understanding the mechanism of each and every gene action are still to be achieved.

Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflict of interests.

Author's contribution

All the authors have equal contribution in writing a manuscript.

Ethics approval: NA.

Consent to participate: NA.

Consent for publication: NA.

REFERENCES

- Abe, H., Urao, T., Ito, T., Seki M. (2003). Arabidopsis AtMYC2 (bHLH) and AtMYB2 (MYB) function as transcriptional activators in abscisic acid signalling. *Plant Cell*. 15: 63-78
- Agarwal, P.K., Agarwal, P., Reddy, M.K., Sopory, S.K. (2006). Role of DREB transcription factors in abiotic and biotic stress tolerance in plants. *Plant Cell Reports*. 25: 1263-1274.

- Agrawal, G.K., Iwahashi, R.R. (2003). Rice MAPKs. *Biochemical and Biophysical Research Communications*. 302: 171-180.
- Avalbaev, M.A., Yuldashev, R.A., Fatkhutdinova, R.A., Urusov, F.A., Safutdinova, Y.V., Shakirova, F.M. (2010). The influence of 24-epibrassinolide on the hormonal status of wheat plants under sodium chloride. *Applied Biochemistry and Microbiology*. 46: 99102.
- Bai, Y., Sunarti, S., Kissoudis, C., Visser R.G.F., van der Linden, C.G. (2018). The role of tomato WRKY genes in plant responses to combined abiotic and biotic stresses. *Frontiers in Plant Science*. 9: 801.
- Bailey-Serres, J., Parker, J.E., Ainsworth, E.A., Oldroyd, G.E.D., Schroeder, J.I. (2019). Genetic strategies for improving crop yields. *Nature*. 575: 109-118
- Bao, W., Wang, X., Chen, M., Chai, T., Wang, H. (2018). AWRKY transcription factor, PcWRKY33, from *Polygonum cuspidatum* reduces salt tolerance in transgenic *Arabidopsis thaliana*. *Plant Cell Reports*. 37:1033-1048
- Bobade, S.S., Dhekane, S.P., Salunke, P.A., Mane, S.G., Dhawan, S.S., Marathe, R.J. and Phatake, Y. B. (2021). Microbes Mediated Mitigation of Abiotic Stresses in Agriculture. *Indian Journal of Agricultural Research*. 1: 11.
- Canter, L.W. (2018). *Environmental Impact of Agricultural Production Activities*. Broken Sound Parkway NW: CRC Press.
- Causier, B., Lloyd, J., Stevens, L., Davies, B. (2012). TOPLESS co-repressor interactions and their conservation in plants. *Plant Signal Behaviour*. 7: 325-328.
- Chen, Z.J. (2012). Ubiquitination in signalling to and activation of IKK. *Immunological Reviews*. 246: 95-106.
- Choi, J. Huh, S.U. Kojima, M., Sakakibara, H., Paek, K.H., Hwang, I. (2010). The cytokinin-activated transcription factor ARR2 promotes plant immunity via TGA3/NPR1-dependent salicylic acid signalling in *Arabidopsis*. *Developmental Cell*. 19: 284-295.
- Choudhury, F.K., Devireddy, A.R., Azad, R.K., Shulaev, V., Mittler, R. (2018). Local and systemic metabolic responses during light-induced rapid systemic signaling. *Plant Physiology*. 178: 1461-1472.
- Cingoz, G.S., Verma, S.K., Gurel, E. (2014). Hydrogen peroxide-induced antioxidant activities and cardiogenic glycoside accumulation in callus cultures of endemic *Digitalis* species. *Plant Physiology and Biochemistry*. 82: 89-94.
- Cuadrado, A. and Nebreda, A.R. (2010). Mechanisms and functions of p38 MAPK signalling. *Biochemical Journal*. 429: 403-417
- Cuenda, A. and Rousseau, S. (2007). p38 MAP-kinases pathway regulation, function and role in human diseases. *Biochimica et Biophysica Acta*. 1773: 1358-1375.
- Das, P., Lakra, N., Nutan, K.K., Singla-Pareek, S.L., Pareek, A.A. (2019). Unique bZIP transcription factor imparting multiple stress tolerance in Rice. *Rice* 12: 58.
- Daszkowska-Golec, A. and Szarejko, I. (2013). The molecular basis of ABA-mediated plant response to drought. In: Vahdati K, Leslie C. (Eds), *Abiotic Stress - Plant Responses and Applications in Agriculture*. Intech Publisher., Rijeka, 103-134.
- Davis, R.J. (2000). Signal transduction by the JNK group of MAP kinases. *Cell*. 103: 239-252.
- Dubos, C., Stracke, R., Grotewold, E., Weisshaar, B., Martin, C., Lepiniec, L. (2010). MYB transcription factors in *Arabidopsis*. *Trends in Plant Science*. 15: 573-581.
- El-Mahi, H., Perez-Hormaeche, J., De Luca, A., Villalta, I., Espartero, J., Gamez-Arjona, F., Fernandez, J.L., Bundo, M., Mendoza, I., Mieulet, D. (2019). A critical role of sodium flux via the plasma Membrane Na⁺/H⁺ exchanger SOS1 in the salt tolerance of rice. *Plant Physiology*. 180: 1046-1065.
- Eulgem, T. and Somssich, I.E. (2007). Networks of WRKY transcription factors in defence signalling. *Current Opinion in Plant Biology*. 10: 366-371.
- Fariduddin, Q., Yusuf, M., Ahmad, I., Ahmad, A. (2014). Brassinosteroids and their role in response of plants to abiotic stresses. *Biologia Plantarum*. 58: 9-17.
- Fedoroff, N.V., Battisti, D.S., Beachy, R.N., Cooper, P.J., Fischhoff, D.A., Hodges, C.N., Knauf, V.C., Lobell, D., Mazur, B.J., Molden, D. (2010). Radically rethinking agriculture for the 21st century. *Science*. 327: 833-834.
- Foyer, C.H. and Noctor, G. (2005). Oxidant and antioxidant signaling in plants: a re-evaluation of the concept of oxidative stress in a physiological context. *Plant Cell Environment*. 28: 1056-1071.
- Furihata, T., Maruyama, K., Fujita, Y., Umezawa, T., Yoshida, R., Shinozaki, K. (2006). Absciscic acid-dependent multisite phosphorylation regulates the activity of a transcription activator AREB1. *Proceedings of the National Academy of Sciences (USA)* 103: 1988-1993.
- Gallo, K.A. and Johnson, G.L. (2002). Mixed-lineage kinase control of JNK and p38 MAPK pathways. *Nature Reviews Molecular Cell Biology*. 3: 663-672.
- Golldack, D., Lu-king, I., Yang, O. (2011). Plant tolerance to drought and salinity: stress regulating transcription factors and their functional significance in the cellular transcriptional network. *Plant Cell Reports*. 30: 1383-1391.
- Gong, W., Shen, Y.P., Ma, L.G., Pan, Y., Du, Y.L., Wang, D.H., Ma, L. (2004). Genome-wide ORFeome cloning and analysis of *Arabidopsis* transcription factor genes. *Plant Physiology*. 135: 773-782.
- Gonzalez, D.H. (2016). Introduction to transcription factor structure and function. In *Plant Transcription Factors*; Elsevier: Amsterdam, The Netherlands. 3-11.
- Gu, L., Wei, H., Wang, H., Su, J., Yu, S. (2018). Characterization and functional analysis of GhWRKY42, a group IId WRKY gene, in upland cotton (*Gossypium hirsutum* L.). *BMC Genetics*. 19:48.
- Guan, L.M., Zhao, J., Scandalios, J.G. (2000). *Cis*-elements and trans-factors that regulate expression of the maize *Cat1* antioxidant gene in response to ABA and osmotic stress: H₂O₂ is the likely intermediary signaling molecule for the response. *Plant Journal*. 22: 87-95.
- Gujjar, R.S., Akhtar, M., Singh, M. (2014). Transcription factors in abiotic stress tolerance. *Indian Journal of Plant Physiology*. 19: 306-316.
- Guo, Y., Halfter, U., Ishitani, M., Zhu, J.K. (2001). Molecular characterization of functional domains in the protein kinase SOS2 that is required for plant salt tolerance. *Plant Cell*. 13: 1383-1400

- Gutha, L.R., Reddy, A.R. (2008). Rice DREB1B promoter shows distinct stress-specific responses and the overexpression of cDNA in tobacco confers improved abiotic and biotic stress tolerance. *Plant Molecular Biology*. 68: 533-555.
- Hasegawa, P.M., Bressan, R.A., Zhu, J.K. and Bohnert, H.J. (2000). Plant cellular and molecular responses to high salinity. *Annual Review of Plant Biology*. 51(1): 463-499.
- Haubrick, L.L., Torsethagen, G., Assmann, S.M. (2006). Effect of brassinolide, alone and in concert with abscisic acid, on control of stomatal aperture and potassium currents of *Vicia faba* guard cell protoplasts. *Physiologia Plantarum*. 128: 134-143.
- Hoehenwarter, W., Thomas, M., Nukarinen, E., Egelhofer, V., Rohrig, H., Weckwerth, W. *et al.* (2013). Identification of novel in vivo MAP kinase substrates in *Arabidopsis thaliana* through use of tandem metal oxide affinity chromatography. *Molecular and Cellular Proteomics*. 12: 369-380.
- Hou, X.M., Zhang, H.F., Liu, S.Y., Wang, X.K., Zhang, Y.M., Meng, Y.C., Luo, D., Chen, R.G. (2020). The NAC transcription factor CaNAC064 is a regulator of cold stress tolerance in peppers. *Plant Science*. 291: 110346.
- Hu, Y., Pandey, A. K., Wu, X., Fang, P. and Xu, P. (2022). The Role of Arbuscular Mycorrhiza Fungi in Drought Tolerance in Legume Crops: A Review. *Legume Research: An International Journal*. 45(1): 1-9.
- Huang, D., Wu, W., Abrams, S.R., Cutler, A.J. (2008). The relationship of drought-related gene expression in *Arabidopsis thaliana* to hormonal and environmental factors. *Journal of Experimental Botany*. 59: 2991-3007.
- Ishitani, M., Liu, J., Halfter, U., Kim, C.S., Wei, M., Zhu, J.K. (2000). SOS3 function in plant salt tolerance requires myristoylation and calcium-binding. *The Plant Cell*. 12: 1667-1677.
- Jain, M. and Khurana, J.P. (2009). Transcript profiling reveals diverse roles of auxin-responsive genes during reproductive development and abiotic stress in rice. *The FEBS Journal*. 276: 3148-3162.
- Ji, H., Pardo, J.M., Batelli, G., VanOosten, M.J., Bressan, R.A., Li, X. (2013). The Salt Overly Sensitive (SOS) pathway: established and emerging roles. *Molecular Plant*. 6: 275-286.
- Johnson, R.R., Wagner, R.L., Verhey, S.D., Walker-Simmons, M.K. (2002). The abscisic acid-responsive kinase PKABA1 interacts with a seed-specific abscisic acid response element-binding factor, TaABF and phosphorylates TaABF peptide sequences. *Journal of Plant Physiology*. 130: 837-846.
- Kocsy, G., Galiba, G., Brunold, C. (2001). Role of glutathione in adaptation and signaling during chilling and cold acclimation in plants. *Journal of Plant Physiology*. 113: 158-164.
- Kotchoni, O.S., Kuhns, C., Ditzer, A., Kirch, H.H., Bartels, D. (2006). Over-expression of different aldehyde dehydrogenase genes in *Arabidopsis thaliana* confers tolerance to abiotic stress and protects plants. *Journal of Plant Physiology*. 29: 1033-1048.
- Li, H., Wu, J., Shang, X., Geng, M., Gao, J., Zhao, S., Yu, X., Liu, D., Kang, Z., Wang, X. (2019). WRKY transcription factors shared by BTH-induced resistance and NPR1-mediated acquired resistance improve broad-spectrum disease resistance in wheat. *Molecular Plant-Microbe Interactions*. 33: 433-443.
- Li, J., Han, G., Sun, C., Sui, N. (2019). Research advances of MYB transcription factors in plant stress resistance and breeding. *Plant Signaling and Behavior*. 14: 1613131.
- Li, Z., Hua, X., Zhong, W., Yuan, Y., Wang, Y., Wang, Z., Ming, R., Zhang, J. (2020). Genome-wide identification and expression profile analysis of WRKY family genes in the autopolyploid *Saccharum spontaneum*. *Plant and Cell Physiology*. 61: 616-630.
- Liang, C., Meng, Z., Meng, Z., Malik, W., Yan, R., Lwin, K.M., Lin, F., Wang, Y., Sun, G., Zhou, T. (2016). GhABF2, a bZIP transcription factor, confers drought and salinity tolerance in cotton (*Gossypium hirsutum* L.). *International Journal of Scientific Reports*. 6: 35040.
- Lilly, J.J. and Subramanian, B. (2019). Gene network mediated by WRKY13 to regulate resistance against sheath infecting fungi in rice (*Oryza sativa* L.). *Plant Sciences*. 280: 269-282.
- Lim, K.H. and Staudt, L.M. (2013). Toll-like receptor signaling. *Cold Spring Harbor Perspectives in Biology*. 5: a011247.
- Liu, C., Mao, B., Ou, S., Wang, W., Liu, L., Wu, Y., Chu, C., Wang, X. (2014). OsbZIP71, a bZIP transcription factor, confers salinity and drought tolerance in rice. *Plant Molecular Biology*. 84: 19-36.
- Ma, D.M., Xu, W.R., Li, H.W., Jin, F.X., Guo, L.N., Wang, J., Dai, H.J., Xu, X. (2014). Co-expression of the *Arabidopsis* SOS genes enhances salt tolerance in transgenic tall fescue (*Festuca arundinacea* Schreb.). *Protoplasma*. 251: 219-231.
- Maser, P., Eckelman, B., Vaidyanathan, R., Horie, T., Fairbairn, D.J., Kubo, M., Yamagami, M., Yamaguchi, K., Nishimura, M., Uozumi, N. (2002). Altered shoot/root NaR distribution and bifurcating salt sensitivity in *Arabidopsis* by genetic disruption of the NaR transporter AtHKT1. *FEBS Letters*. 531: 157-161.
- Millard, P.S., Kragelund, B.B., Burow, M. (2019). R2R3 MYB transcription factors-functions outside the DNA-binding domain. *Trends in Plant Science*.
- Mittler, R. (2002). Oxidative stress, antioxidants and stress tolerance. *Trends in Plant Science*. 7: 405-410.
- Morrison, D.K. (2012). MAP kinase pathways. *Cold Spring Harbor Perspectives in Biology*. 4: a011254.
- Munemasa, S., Oda, K., Watanabe-Sugimoto, M., Nakamura, Y., Shimoishi, Y. (2007). The coronatine-insensitive 1 mutation reveals the hormonal signalling interaction between abscisic acid and methyl jasmonate in *Arabidopsis* guard cells. Specific impairment of ion channel activation and second messenger production. *Plant Physiology*. 143: 1398-1407.
- Munns, R. (2002). Comparative physiology of salt and water stress. *Plant, Cell and Environment*. 25: 239-250.
- Mustafa, G., Joyia, F.A., Anwar, S., Parvaiz, A., Khan, M.S. (2018). Biotechnological interventions for the improvement of sugarcane crop and sugar production. *Sugarcane-Technology and Research*. IntechOpen: London, UK.113-138.
- Newton, K., Dixit, V.M. (2012). Signaling in innate immunity and inflammation. *Cold Spring Harbor Perspectives in Biology*. 4: a006049.
- Nijhawan, A., Jain, M., Tyagi, A.K., Khurana, J.P. (2008). Genomic survey and gene expression analysis of the basic leucine zipper transcription factor family in rice. *Journal of Plant Physiology*. 146: 333-350.

- Niu, C.F., Wei, W., Zhou, Q.Y., Tian, A.G., Hao, Y.J., Zhang, W.K. (2012). Wheat WRKY genes TaWRKY2 and TaWRKY19 regulate abiotic stress tolerance in transgenic Arabidopsis plants. *Plant Cell and Environ.* 35: 1156-1170.
- Ooka, H., Satoh, K., Doi, K., Nagata, T., Otomo, Y., Murakami, K., Hayashizaki, Y. (2003). Comprehensive analysis of NAC family genes in *Oryza sativa* and *Arabidopsis thaliana*. *DNA Research*. 10: 239-247.
- Pistelli, L., Iacona, C., Miano, D., Cirilli, M., Colao, M.C., Mensuali-Sodi, A. (2012). Novel *Prunus* rootstock somaclonal variants with divergent ability to tolerate waterlogging. *Tree Physiology*. 32: 355-368.
- Pospisil, P. (2016). Production of reactive oxygen species by photosystem II as a response to light and temperature stress. *Frontiers in Plant Science*. 7:1950.
- Qin, Y., Wang, M., Tian, Y., He, W., Han, L., Xia, G. (2012). Over-expression of TaMYB33 encoding a novel wheat MYB transcription factor increases salt and drought tolerance in *Arabidopsis*. *Molecular Biology Reports*. 39: 7183-7192.
- Qiu, Q., Guo, Y., Dietrich, M., Schumaker, K.S., Zhu, J.K. (2001). Characterization of the plasma membrane Na⁺/H⁺ exchanger in *Arabidopsis thaliana*. *Madison, Wisconsin: International workshop on plant membrane biology, 12th, pp: 235.*
- Rahman, H., Ramanathan, V., Nallathambi, J., Duraialagaraja, S., Muthurajan, R. (2016). Over-expression of a NAC 67 transcription factor from finger millet (*Eleusine coracana* L.) confers tolerance against salinity and drought stress in rice. *BMC Biotechnology*, 16(1): 7-20.
- Rayapuram, N., Bigeard, J., Alhoraibi, H., Bonhomme, L., Hesse, A.M., Vinh, J., Pflieger, D. (2018). Quantitative phosphoproteomic analysis reveals shared and specific targets of *Arabidopsis* mitogen-activated protein kinases (MAPKs) MPK3, MPK4 and MPK6. *Molecular and Cell Proteomics*. 17: 61-80.
- Rhind, N. and Russell, P. (2012). Signaling pathways that regulate cell division. *Cold Spring Harbor Perspectives in Biology*. 4: a005942.
- Rodriguez, Limardo, R.G., Ferreira, D.N., Roitberg, A.E., Marti, M.A., Turjanski, A.G. (2011). p38g activation triggers dynamical changes in allosteric docking sites. *Biochemistry*. 50: 1384-1395.
- Romero, Puertas, M.C., Rodriguez, Serrano, M., Corpas, F.J., Gomez, M.D., Del, Rio, L.A., Sandalio, L.M. (2004). Cadmium induced subcellular accumulation of O₂ and H₂O₂ in pea leaves. *Plant Cell and Environment*. 27: 1122-1134.
- Roychoudhury, A., Paul, S., Basu, S. (2013). Cross-talk between abscisic acid-dependent and abscisic acid-independent pathways during abiotic stress. *Plant Cell Reports*. 32: 985-1006.
- Sah, S.K., Reddy, K.R., Li, J. (2016). Abscisic acid and abiotic stress tolerance in crop plants. *Frontiers in Plant Science*. 7: 571.
- Sairam, R.K., Kumutha, D., Ezhilmathi, K., Deshmukh, P.S., Srivastava, G.C. (2008). Physiology and biochemistry of waterlogging tolerance in plants. *Journal of Plant Biology*. 52: 401-412.
- Sheard, L.B., Tan, X., Mao, H., Ben-Nissan, G., Hinds, T.R. (2010). Jasmonate perception by inositol-phosphate potentiated COI1-JAZ co-receptor. *Nature*. 468: 400.
- Shimono, M., Sugano, S., Nakayama, A., Jiang, C.J., Ono, K., Toki, S. (2007). Rice WRKY45 plays a crucial role in benzothiazole-inducible blast resistance. *The Plant Cell*. 19: 2064-2076.
- Singh, M., Choudhary, A., Kumar, A., Thapa, S. (2021c). Genetically modified food: their problems and promise. *Biotica Research Today*. 3(2): 111-113.
- Singh, M., Nara, U., Kumar, A., Choudhary, A., Singh, H., Thapa, S. (2021a). Salinity tolerance mechanisms and their breeding implications. *Journal of Genetic Engineering and Biotechnology*. 19(1): 1-18.
- Singh, M., Nara, U., Kumar, A., Thapa, S., Jaswal, C., Singh, H. (2021b). Enhancing genetic gains through marker-assisted recurrent selection: from phenotyping to genotyping. *Cereal Research Communications*. 1-16.
- Spiteller, P., Kern, W., Reiner, J., Spiteller, G. (2001). Aldehydic lipid peroxidation products derived from linoleic acid. *Biochimica et Biophysica Acta Molecular Cell Biology and Lipids*. 1531: 188-208.
- Suhita, D., Kolla, V.A., Vavasseur, A., Raghavendra, A.S. (2003). Different signalling pathways involved during the suppression of stomatal opening by methyl jasmonate or abscisic acid. *ThrePlant Science*. 164: 481-488.
- Suhita, D., Raghavendra, A.S., Kwak, J.M., Vavasseur, A. (2004). Cytoplasmic alkalization precedes reactive oxygen species production during methyl jasmonate-and abscisic acid-induced stomatal closure. *Journal of Plant Physiology*. 134: 1536-1545.
- Szemenyei, H., Hannon, M., Long, J.A. (2008). TOPLESS mediates auxin-dependent transcriptional repression during *Arabidopsis* embryogenesis. *Science*. 319: 1384-1386.
- Tanaka, Y., Sano, T., Tamaoki, M., Nakajima, N., Kondo, N., Hasezawa, S. (2006). Cytokinin and auxin inhibit abscisic acid induced stomatal closure by enhancing ethylene production in *Arabidopsis*. *Journal of Experimental Botany*. 57: 259-266.
- Tanaka, Y., Sano, T., Tamaoki, M., Nakajima, N., Kondo, N., Hasezawa, S. (2005). Ethylene inhibits abscisic acid-induced stomatal closure in *Arabidopsis*. *Journal of Plant Physiology*. 138: 2337-2343.
- Turkan, I. And Demiral, T. (2009). Recent developments in understanding salinity tolerance. *Environmental and Experimental Botany*. 67: 2-9.
- Ulker, B. and Somssich, I.E. (2004). WRKY transcription factors: from DNA binding towards biological function. *Curr. Opin. Journal of Plant Biology*. 7: 491-498.
- Uluhan, E., Kele, S., Tufan, F. (2019). Analysis of WRKY transcription factors in barley cultivars infected with *Fusarium culmorum*. *International Journal of Life Science and Biotechnology*. 2: 165-174.
- Umezawa, T., Sugiyama, N., Mizoguchi, M., Hayashi, S., Myouga, F., Yamaguchi-Shinozaki, K. (2009). Type 2C protein phosphatases directly regulate abscisic acid-activated protein kinases in *Arabidopsis*. *Proceedings of the National Academy of Sciences U.S.A.* 106: 17588-17593.
- Vaughan, M.M., Block, A., Christensen, S.A., Allen, L.H., Schmelz, E.A. (2018). The effects of climate change associated abiotic stresses on maize phytochemical defenses. *Phytochemistry Reviews*. 17: 37-49.

- Vishwakarma, K., Upadhyay, N., Kumar, N., Yadav, G., Singh, J., Mishra, R.K. (2017) Absciscic acid signaling and abiotic stress tolerance in plants: a review on current knowledge and future prospects. *Frontier in Plant Science*. 8: 161.
- Wang, C.T., Ru, J.N., Liu, Y.W., Yang, J.F., Li, M., Xu, Z.S., Fu, J.D. (2018). The maize WRKY transcription factor ZmWRKY40 confers drought resistance in transgenic Arabidopsis. *International Journal of Molecular Science*. 19: 2580.
- Waqas, M.A., Khan, I., Akhter, M.J., Noor, M.A., Ashraf, U. (2017). Exogenous application of plant growth regulators (PGRs) induces chilling tolerance in short-duration hybrid maize. *Environmental Science and Pollution Research* 24: 11459-11471.
- Wasternack, C. (2007). Jasmonates: An update on biosynthesis, signal transduction and action in plant stress response, growth and development. *Annals of Botany*. 100: 681-697.
- Xiong, L. and Yang, Y. (2003). Disease resistance and abiotic stress tolerance in rice are inversely modulated by an abscisic acid-inducible mitogen-activated protein kinase. *The Plant Cell*. 15: 745-759.
- Xiong, L. and Zhu, J.K. (2002). Molecular and genetic aspects of plant responses to osmotic stress. *Plant Cell and Environment*. 25: 131-139.
- Xiong, W., Xu, X., Zhang, L., Wu, P., Chen, Y., Li, M., Jiang, H., Wu, G. (2013). Genome-wide analysis of the WRKY gene family in physic nut (*Jatropha curcas* L.). *Gene*. 524: 124-132.
- Xiong, Y., Liu, T., Tian, C., Sun, S., Li, J., Chen, M. (2005). Transcription factors in rice: A genome-wide comparative analysis between monocots and eudicots. *Plant Molecular Biology*. 59: 191-203.
- Yang, S.L., Lan, S.S., Gong, M. (2009). Hydrogen peroxide-induced proline and metabolic pathway of its accumulation in maize seedlings. *Journal of Plant Physiology*. 166: 1694-1699.
- Zafar, S.A., Noor, M.A., Waqas, M.A., Wang, X., Shaheen, T., Raza, M., Rahman, M.U. (2018). Temperature extremes in cotton production and mitigation strategies. Past, present and future trends in cotton breeding. 65-91.
- Zhang, L., Zhao, G., Jia, J., Liu, X., Kong, X. (2012). Molecular characterization of 60 isolated wheat MYB genes and analysis of their expression during abiotic stress. *Journal of Experimental Botany*. 63: 203-214.
- Zhang, Q., Li, J., Zhang, W., Yan, S., Wang, R., Zhao, J. (2012b). The putative auxin efflux carrier OsPIN3t is involved in the drought stress response and drought tolerance. *The Plant Journal*. 72: 805-816.
- Zhang, X., Zhang, L., Dong, F., Gao, J., Galbraith, D.W., Song, C.P. (2001). Hydrogen peroxide is involved in abscisic acid-induced stomatal closure in *Vicia faba*. *Journal of Plant Physiology*. 126: 1438-1448.
- Zhao, Z., Chen, G., Zhang, C. (2001). Interaction between reactive oxygen species and nitric oxide in drought-induced abscisic acid synthesis in root tips of wheat seedlings. *Australian Journal of Plant Physiology*. 28: 1055-1061.
- Zhou, W., Lozano-Torres, J.L., Bilou, I., Zhang, X., Hai, Q., Smart, G., (2019). A jasmonate signaling network activates root stem cells and promotes regeneration. *Cell*. 177: 942.e14-956.e14.
- Zhu, J.K. (2001). Plant salt tolerance. *Trends in Plant Science*. 6: 66-71.
- Zhu, J.K. (2016). Abiotic stress signaling and responses in plants. *Cell*. 167: 313-324.
- Zhu, M., Meng, X., Cai, J., Li, G., Dong, T., Li, Z. (2018). Basic leucine zipper transcription factor SlbZIP1 mediates salt and drought stress tolerance in tomato. *BMC Plant Biology*. 18: 83.
- Zorb, C., Geilfus, C.M., Dietz, K.J. (2019). Salinity and crop yield. *Journal of Plant Biology*. 21: 31-38.
- Zouine, M., Fu, Y., Chateigner-Boutin, A.L., Mila, I., Frasse, P., Wang, H., Audran, C., Roustan, J.P., Bouzayen, M. (2014). Characterization of the tomato ARF gene family uncovers a multi-levels post-transcriptional regulation including alternative splicing. *PLoS One*. 9: e84203.