Diverse Aspects of ABA Signaling under Drought Stress in Wheat

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Abstract: Wheat is one of the oldest cultivated crops existed from the early ancient times. Incread temperatures show that drought has become one of the major environmental stresses which seriously restricts the global wheat production by causing a fluctuation in harvest amount. There are numerous breeding efforts by using new biotechological tools to avoid negative effects of drought, including changes in gene expression of some pivotal genome regions, induced signaling pathways, increased antioxidant activity, enhanced compatible solutes and osmoprotectant proteins, etc. To afford the water scarcity, abscisic acid (ABA), a plant growth regulator, has an important role on these internal responses. ABA levels increase during drought stress, accompanied by major changes in gene expression. After increased ABA levels, a signal cascade transported to the leaves triggers the stomatal closure to prevent extra evaporation of water. An activation of several stress signaling factors and corresponding changes become more visible. Physiological studies combined with the molecular approaches help to dissect several exact strategies for unlocking the ABA signal pathways during drought stress. From these aspects, this review summarizes the ABA related studies under drought stress in wheat and the role of ABA related intermediate molecules at cell level.

Keywords: Abscisic acid, Drought, Plant stress tolerance, Signaling, Wheat.

INTRODUCTION

Wheat is an important cereal grown under the pressure of different kinds of environmental stresses from east to the west part of the world. One of the most important factors affecting the wheat yield is well known to be drought. Owing to rise in the average temperature of climate, 20th century was recorded more common for drought [1]. In time, drought stress has changed its effects from minor to major by reducing the crop yield to a lower level. So, every drop of water gained much more importance for agricultural practices and sustainable food security [2].

Drought can be defined as an absence of rainfall or irrigation for a period of time and ultimately the loss of soil moisture [3]. In this respect, drought tolerance in viable agriculture is the ability of a crop to continue the growth and give grains under water-limited conditions [4]. Drought tolerant plants carry a variety of signal pathways and gene regions to cope with dry environment effects. The first response of plant cells under drought stress is induced by osmotic shock. During exposure to osmotic stress, cellular and molecular adaptation occurred as a consequence of internal signal molecules. Further, stress triggers several changes in the profiles of metabolites such as compatible solutes, proteins, antioxidants, phytoalexins and cryoprotectans [5]. At the same time, early responses to water deficit include increasing the level of the plant growth regulators such as abscisic acid, and decreasing the leaf transpiration and photosynthesis rate. Signaling molecules delivered from roots to leaf tissues through vascular transport system under water deficit are managed by more than one signal mechanism. The major signal molecule is abscisic acid, even though jasmonic acid, ethylene, and calcium also act as signal molecules [6]. ABA allows the communication between the root and above-ground part, which needs to adapt to drought conditions [7]. At this point, ABA acts at multiple cellular levels to protect the plants against to negative effects of drought, including the regulation of stomatal aperture and the activation of gene expression.

This review focuses on the role of endogenous and exogenous ABA behaviour and its relationship with various drought-related molecules under drought in wheat. Also, the conspicuous points of ABA signaling and signal based triggering pathways which are closely connected with drought stress in wheat are highlighted. It is important to make comparisons between different approaches to open a new perspective in plant signaling and crop stress tolerance. Thus, it is estimated that the components of ABA signalling mechanism can be quickly adapted to new generation technologies for paving more tolerant crops.

REGULATION OF ABA BIOSYNTHESIS BY OSMOTIC ADJUSTMENT

Soil drought is the major reason of osmotic stress in plants. Osmotic stress caused by drought enables plant survival and gives rise to decline in carbon assimilation, which is related to a physiological closure of leaf

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stomata and to drag the cell into a lower photosynthetic activity [8]. At this point, ABA has an important role in the plant resistance mechanism for ensuring the stable osmotic stress caused by soil drought. It is required for stomatal closure under drought conditions to prevent the intracellular water loss and also necessary for the inhibition of germination process in plants [9,6]. After sensing dryness, root tissues release ABA to deliver the water deficit signal towards to the leaves. ABA is transported through xylem sap to the shoots, and then it closes stomata, reduces transpiration, and loses leaf turgor [10-12]. Thus, various biochemical reactions are induced in the guard cells and caused to decrease of stomatal conductance [13]. Signal for turgor reaction in guard cells quickly starts with ABA hormone [14]. First, cytosolic calcium concentration increased by an external ABA signal and this triggering maintains both slow-activating (S-type) and rapid transient (R-type) anion channels [15,16]. Thus, membrane potential of the guard cells becomes more alkali. Releasing anions from guard cells caused depolarization by providing a K^+ efflux to the outside of the cell. Guard cell turgor pressure decreases via efflux of potassium which leads the stomatal closure.

Drought resistant plants can be screened and identified under osmotic stress induced by PEG in hydroponics [17]. The growth of seedlings in solutions containing Hoagland medium with high osmotic potential (*e.g.* PEG 6000) induce osmotic stress. After seven days of PEG treatment on wheat seedlings, leaf ABA content increased four-fold in susceptible cultivar (SQ1) and seven-fold in resistant cultivar (CS) in comparison to control [18]. The dramatic drop in leaf osmotic potential may result in increase of leaf ABA content. The higher ABA level in the tolerant cultivar improved its stress tolerance through stomata closure reducing transpiration and improving water relations, and alleviates the negative effects of stress on the yield. Addition of 0.1 μM ABA to the nutrient solution containing PEG did not increase endogenous leaf ABA levels compared to PEG treatment. However, ABA increased proline and carbohydrate content and thus, the harmful effects of osmotic stress reduced through osmotic adjustment. In PEG-treated plants growing until the harvest, a greater decrease of yield components was detected in susceptible cultivar (SQ1) than in resistant cultivar (CS). PEG and exogenous ABA caused a greater increase of these yield parameters in CS compared to SQ1. The long-term healing effect of ABA under osmotic stress is succeeded through ABA-mediated transcriptional regulation of number of genes.

ABA SIGNAL CASCADE

ABA levels are induced in response to various stress signals. Plants including higher endogenous abscisic acid content can overcome more successfully the negative effects of water stress [19]. Plant physiological responses to ABA are generated by changes in gene expression and post-translational modifications [6, 14, 99].

ABA uptake and transfer between cells are stimulated by an ATP-dependent transporter protein and enable an active carrier path for abscisic acid in plant cells under abiotic stress conditions. Signal receptors and their perception accepted as the first initiators of complex set of signal cascades which turn the lights on for a specific signal transduction regulated by gene expression [20]. Transcription factors are the major players of ABA signal cascade which is to be known more responsive elements to ABA signaling and drought. ABA-regulated genes contain binding sites for proteins of the MYB and MYC families and also both bZIP and ABF2 are prominent transcription factors of positive ABA regulators [21].

CANDIDATE SECONDARY MESSENGERS IN ABA SIGNALING

A crosstalk signaling between secondary messengers modulates the activity of specific proteins that act at the genome level to control the expression of defense/response genes. Second messengers, including Ca^{2+}, cyclic ADP ribose (cADPR), inositol 1, 4, 5 trisphosphate (InsP3), inositol hexaphosphate (InsP6) and H_2O_2 are implicated in ABA-mediated signaling. Also, ABA responses are interrupted by lipid-derived signals, pH and redox signals which have important roles on intracellular signaling [13, 22-24]. For phospholipid cleavage, several types of phospholipases are activated by ABA to generate lipid messengers like InsP3, diacyglycerol (DAG) etc. Phospholipids, as second messengers, are good switches for regulating calcium dependent protein kinases (CDPKs) activity which is under the control of plant hormone ABA. InsP3 is a cytosolic second messenger which stimulates Ca^{2+} to release from the endoplasmic reticulum. Under hyperosmotic stress, various plants increased the IP3 levels for an initial response [25].

Calcium is a necessary divalent cation essential for strengthening the plant cell walls and root elongation. Additionally, it is required for membran formation by bridging phosphate and carboxyl groups of phospholipids [26]. Calcium acts as a mediator by providing a close cross talk between ABA-dependent and ABA independent pathways and exhibits a rapid increase in plant cells during stress conditions [27]. Under drought stress, transferring the calcium ions from vacuole and extracellular spaces into the cytocol increases cytosolic calcium concentration in the ABA-treated guard cells. In this way, calcium ions activate inward anion channels by suppressing the inward potassium channels [14]. Ca^{2+} influx into the cell cytoplasm is transient and controlled by calcium-dependent protein kinases (*CDPK*s) sensor molecules. Ca^{2+} dependent signaling leads to the activation of late embryogenesis abundant (LEA) type gene (such as the DRE/CRT class of genes). *LEA* protein accumulation found under the conditions of extreme desiccation in higher plants [28].

ABA-BINDING SPECIFIC KEY PROTEINS

ABA is a potential target for anion channels by constructing an ABA-receptor complex [29]. Under feasible environmental conditions, several kinds of proteins are primarily synthesized by plants not only for complex pathways but also they are released as basic mediators for survival of the cell. Several plasma membrane proteins and intracellular receptors have been described for ABA sensing [30, 31]. One of the examples belonging to drought specific protein group is known as LEA (Late Embryogenesis Abundant) family. These proteins are highly hydrophilic and have the ability to bind water molecules. Expression level of LEA proteins highly induced during drought and osmotic stress [19, 32].

ABA induces synthesis of some LEA proteins and LEA proteins have roles in processes related to desiccation tolerance of plant seeds during their late stages of development. They also accumulate in vegetative tissues during dehydration stress [33, 34]. Most genes encoding LEA proteins have an abscisic acid response element (ABRE) in their promoters which are induced by abscisic acid [35, 36]. Higher ABA content in leaves of non-stressed young wheat plants is related to earlier expression of basic LEA II (WZY2) and LEA III (TaLEA2 and TaLEA3) proteins as a part of the adaptive response to progressive drought stress [37]. Vaseva and her colleagues also showed that higher ABA content, early immunodetection of dehydrins, and a significant increase of WZY2 transcript levels in drought-stressed leaves of the tolerant winter wheat variety. High expression levels of some acidic dehydrin genes (WCOR410b, TADHN) were detected in leaves under drought stress during early vegetative development. Neutral WZY2 dehydrin, TaLEA2 and TaLEA3 transcripts accumulated gradually with the progress of drought stress.

Ion channels are suggested to act as osmo-regulatory feedback sensors that are activated by stretching of the plasma membrane. Until now, a number of ionic channels have been identified in cell protoplasts and vacuole membranes. Tonoplast ion channels established on stomatal aperture and regulated by ABA [38]. A number of ion channels embedded in the membranes of guard cells and vacuoles. Inward and outward rectifying potassium channels on the guard cell membranes mediate both efflux and influx potassium and activated by ABA [6]. In stomata, ion channels on guard cells quickly turn on after ABA signaling. An OST1 construct a reciprocal cross talk between SLAC1 and KAT1 anion channel receptors. As a result, ABA signal manages the phosphorylation of KAT1 and regulated by ion flow [39]. Another stress protein belongs to Aquaporin (AQP) family. They are located on the plasma membrane and tonoplast. Aquaporins enable cell membrane pores into an optimal formation [40].

Plant ABC transporters are a large group of proteins and includes more than 100 proteins that transport various metabolites or signaling molecules, involving phytohormones, in an ATP dependent manner [41, 42]. ABC proteins are common plant transporters which were also involved in the process of detoxification. Except these functions, ABC proteins are also responsible for other plant metabolic pathways such as surface lipid deposition, phytate accumulation in seeds, and transport of abscisic acid. Recently, Krattinger *et al* [43] has been identified a putative ABC transporter protein involved in plant-pathogen interactions.

ABA DEPENDENT AND INDEPENDENT (*DREB1, DREB2*) PATHWAYS FOR STRESS TOLERANCE

ABA-dependent and ABA-independent pathways are involved in the osmotic stress process [44]. Drought responsive genes are induced by activators of ABA-dependent and ABA-independent pathways. The promotor regions of many ABA responsive genes have major cis-sequences commonly known as ABRE. The cis-element was first defined in wheat as *Em* gene and found in different plants such as maize, rice and Arabidopsis. Many *cis*-elements known as ABREs have been identified from the promoter analysis of ABA-regulated genes.

Plants have two types of ABA-dependent regulatory pathways [45]. Basic leucine zipper/ABA-responsive element (bZIP/ABRE) is the first defined one [46]. An ABRE/ABPF complex which is a kind of bZIP transcription factor binds to ABRE sequence for activating ABA-responsive gene expression. Hence, ABA signal pathway is completed with the gene expression induction. In Arabidopsis, ABRE binds to several leucine zipper transcription factors such as ABF and ABI5 [47, 46]. ABA is also mediated the induction of RD22 gene by binding the MYC2 and MYB2 transcription factors during drought response [48, 23].

Aside from two ABA-responsive elements (ABREs), drought inducible gene promotors include the dehydration-responsive element (DRE). These elements are managed by ABA dependent and ABA independent signal pathways [49, 24]. Research for DREB-like genes in cereal crops conducted for several plants such as bread wheat [50] and durum wheat [51]. All DREB genes have feature of three conserved regions, EREBP/AP2 DNA binding domain, an N-terminal nuclear localization signal, and conserved Ser/Thr rich region adjacent to the EREBP/AP2 domain. Evaluation under closer-to-real field conditions has concluded that DREB1A in wheat delays development in transgenic plants but does not result in greater biomass accumulation or better grain yield than the control under water stress [52].

DREB transcription factors play key roles in plant stress signaling transduction pathway, they can specifically bind to DRE/CRT element (G/ACCGAC) and activate the expression of many drought stress inducible genes. DRE/CRT is a cis element that is characterized in the Arabidopsis RD9 gene promotor region. The research in ABA hypersensitive mutants of Arabidopsis indicated that ABA dependent and independent pathways showed well correlation with three newly identified mutants which had hot ABA-deficiency suppressors under drought [53]. Additionally, an Arabidopsis ABA-hypersensitive mutant of hat1 has ABA dependent pathways conferred to xerothermic stress [54].

UP AND DOWN REGULATED GENE EXPRESSION FOR ABA ACTIVATION

Drought tolerance is a quantitative character which is under the multiple gene control [55]. To date, changes in gene expression which is driven by drought and its close relatives referred as salt, heat and cold has been studied in many plant species [56-58]. One of the last approaches of Rampino *et al* [59] used the combined effects of both heat and drought stress and found seven up-regulated drought and heat related genes. Expression of many genes is induced by drought and their function of gene products are also directly studied in stress tolerance, regulation of gene expression and signal transduction in stress responses [60]. Timely expression of stress-responsive genes is crucial for the plants. Generally, transcript profiling method is used for dehydration stress occurred during drought, salt and low temperature conditions. Both induced and repressed genes are related to ABA response covers dehydrins, reactive oxygen species, compatible solutes, transcription factor, phospholipid signaling etc. Repressed genes mostly related to growth, cell wall, ribosomal, plasma membrane, and chloroplast proteins. Drought stress up-regulated genes are divided into two main groups. In the first group, genes are responsible for protecting the cells and organs against stress by using their catalytic activities, while others include encoded proteins for signal transduction and gene expression regulation [23]. Water and ion channel proteins, enzymes responsible for formation of compatible solutes, molecular chaperons, late embryogenesis abundant proteins and reactive oxygen-scavening enzymes are directly defined in the first group.

After treatment with ABA, an initial change occurs in the promoter regions of genes which include cis and trans-acting elements. ABA induced gene expression related with promoter derived regions were studied in the previous reports of corresponding plants such as Rab16A (*Oryza sativa*) [61], EM (*Triticum aestivum*) [62], rab28 (*Zea mays*) [63], HVA22 (*Hordeum vulgare*) [64]. Also, various ABA-regulated genes have been identified in different plant species such as *Arabidopsis* [65] and wheat [66]. Moreover, expressions of ABF/ABI5/AREB [47, 9, 46], RD22BP, AtMyb2 [67, 48], CBF/DREB gene family [68, 69] were reported as a result of ABA induction.

Wrab17 and *Wdhn13* genes, belongs to the Cor (cold-responsive)/Lea (late-embryogenesis-abundant) gene family, are responsive to exogenous ABA and drought-stress treatment in *Ae. tauschii* as well as common wheat [70, 71]. *TaDREB1*, *WABI5* and *TaOBF1genes* have roles as a transcription factors for these genes. *Cor*/*Lea* expression was ABA-responsive [71]. The more tolerant accession of *Ae. tauschii* tended to accumulate more abundant transcripts of the *Wrab17, Wdhn13 TaDREB1*, *WABI5* and *TaOBF1genes* than the sensitive accession under drought conditions. Synthetic wheats with high drought tolerance showed significantly higher ABA sensitivity than drought-sensitive synthetic lines.

Among the members of ABA activated protein kinase family, SnRK2 is an important protein kinase which is also activated by osmotic stress. This hyper induction of stress responsive gene expression detected for *Arabidopsis* [72]. PKABA1 is an ABA-inducible gene encoding a SnRK2 member and isolated from wheat [73]. It was also indicated that ABA-induced protein kinase1 (PKABA1) of wheat, as a wheat SnRK2 ortholog, and *Triticum aestivum* ABRE binding factor (TaABF) have the highest sequence and structural similarity to the *Arabidopsis* ABA response protein ABI5 [74]. However, PKABA1, located on the long arm of choromosome 2 in wheat, gene expression is induced by dehydration, cold, and salt stress [75, 76]. As a physiological substrate of PKABA1, transcript levels of TaABF1 were not significantly altered by exogenous ABA application [77].

Gene expression profiles of master compatible solutes which were related to osmolyte pathways and enzymes involved in ABA biosynthesis found as up-regulated after drought stress and they were showed clear differences between durum and bread wheat cultivars. In the transcriptomic profiling work, Aprile *et al* [56] indicated that the expression of 9-cis-epoxycarotenoid-dioxygenase (NCED) which is one of the key enzymes for ABA biosynthesis and pyrroline-5-carboxylate reductase (P5CR) showed strong up-regulation after drought stress application in all genotypes. On the other hand, in the same study ornithine cyclodeaminase was preferentially expressed and up-regulated by drought in bread wheat genotypes.

Negative regulators of ABA-induced responses include some members of type 2C protein phosphatase. Inhibition of PP2C function starts after perception of receptors PYR/PYL/RCAR family. In the presence of ABA hormone, PYR/PYL/RCAR-ABA complex is constructed to inactivate the PP2C which is also inhibited by phosphatidicacid-ABA1 (Abscisic Acid Insensitive 1). A SNF1-related protein kinase (SnRK2) subsequently phosphorylates and interacts with ABA-responsive element binding factor (ABF). These close interactions resulted as an induction of ABA gene expression [21]. The ABI-induced genes include both positive and negative regulators of ABA signaling. ABI1 (Abscisic Acid Insensitive 1) and it's homolog ABI2 (Abscisic Acid Insensitive 2) exhibit high affinity to the ABA binding site and generate negative effectors for ABA responses [39].

Alterations in gene expression levels of several factors can definitely impact on responses to drought [78]. In response to drought stress, [79] found aquaporins expressed as two fold more in addition to some novel gene expression in wheat. Global transcriptomes of guard cells were compared to gene expression in leaves and approximately 300 genes showing ABA regulation unique to guard cells were defined by [80]. Additionally, ABI4 and ABI5 are putative transcription factors directly affected by ABA-regulated gene expression [81]. Protein phosphates 2C is synthesized by ABI1 and ABI2 and dephosphorylation of this PP2C protein may regulate ABA-mediated gene expression [46]. In another study, beta-xanthophylls violaxanthin and neoxanthin are biosynthetic precursors of ABA encoding enzymes in wheat and up-regulated by drought [56].

ABA regulated gene expression was investigated in *Arabidopsis* mutants and one of the knock mutants of corresponding Atabcg40 gene up-regulated under drought stress conditions for ABA import [82]. In rice, genes related to Zn-finger, AP2 transcription factors, protein kinases including MAPK family found as specifically induced by drought [83]. Wheat C_2H_2 zinc finger transcription factor TaZFP15 contains two C_2H_2 zinc finger domains and each one has a conserved motif QALGGH. TaZFP15 expression was up-regulated by drought stress [20]. Since the up-regulation of particular genes has an important effect on plant growth and stress response, down regulated gene expression is also observed for limited number of processes such as genes related to photosynthesis and accumulation of some histone proteins [19, 84].

INTERACTIONS BETWEEN COMPATIBLE SOLUTES AND ABA

A numerous variety of small molecule compounds synthesized as osmoprotectans called compatible solutes to tolerate the drougth stress in plants. In this way, plants protect cellular components against to negative effects of stress [85]. Until now, different kinds of compatible solutes such as glycine betaine, 3-dimethylsulfonopropionate, proline, fructose, mannitol sucrose, trehalose and their high solubility in water has been reported as a subtitute for water molecules released from leaves. Osmotic pressure which is closely related to cellular homeostasis is increased by the high concentration of compatible solutes in stress-prone environments [86]. Due to their hydrophilic nature, compatible solutes move to nucleic acids, proteins and membranes and replace with water molecules around of these targets during water shortages [87].

Plant cell wall is a physical barrier for a wide protection plant cells during abiotic and biotic stress conditions [88]. Supposing that, when the cell enters a dehydration phase, rigid cell wall structure helps to hold a stable protection for the cell water shell [89]. Certain new metabolites synthesized as common biochemical adaptation during osmotic adjustment [90, 91]. Osmolytes are highly soluble molecules defied as non-toxic at huge concentrations and they provide a quick capturing of water molecules. Sugar molecules are belong the group of osmolytes which accumulate to prevent membrane fusion under drought stress [92] .

THE APPLICATION OF EXOGENOUS ABA AND ITS CONTRIBUTIONS TO DROUGHT TOLERANCE

The response to exogenous ABA treatment during drought stress differs in sensitive and tolerant wheat varieties [93]. Exogenous ABA application improved the growth of tolerant variety (sakha 93) through the induction of enzymatic 2 (catalase) and non-enzymatic (carotenoid) systems. ABA ameliorate the negative effects of drought on the growth of sakha 94 by protecting the plasma membrane integrity and higher relative water content, transpritaion rate and lower electrolyte leakage. On the other hand, ABA treatment enhanced disruption of plasma membranes and decrease in PSII activity of sensitive variety (sakha 94). ABA may induce the enzymatic antioxidant system to depress the inhibitory effect of ROS on the plasma membrane and hence improve the growth.

Development of wheat mutants with increased sensitivity to ABA has been one of the essential issues to improve drought tolerant genotypes. Wheat plants with increased ABA sensitivity can be isolated by screening response to different ABA doses in seed germination. Mutants exhibit altered response to different ABA levels. Wheat mutants with increased sensitivity to ABA was identified and referred as wheat *ABA responsive mutants* (*Warm*) by Schramm et. al. [94]. Their efficiency was evaluated in terms of increasing resistance to drought stress. It is estimated that ABA hypersensitive mutants close their stomata at lower concentrations of ABA and thus have higher transpiration efficiency under drought stress (4H, 17H).

Under water deficit condition, imbalance of synthesis/ degradation of D1 protein may occur in wheat. D1 protein in thylakoids of chloroplast is an essential part of the structure and function of photosystem II (PSII) complex [95]. D1 protein encoded by *psbA* gene has an important role in the replacement of injured D1 protein by newly synthesized one [31]. The turnover of D1 protein can be forced to ameliorate the PS II function [96]. The resent study on PEG induced drought stress and effect of exogenous ABA on *psbA* expression during grain filling period showed that PEG stress decreased transcription of *psbA* gene and application of exogenous ABA increased *psbA* transcription, especially in the drought-tolerant cultivar, Shaanmai 5 [80]. The expression of *psbA* gene was closely related to drought stress resistance subject to wheat cultivar. Compared to weak resistance to drought of the cultivar (Yumai 949), Shaanmai 5 received less damage in plasma membranes and less reduces in relative water content, chlorophyll content, yield, and *psbA* transcriptional level in the PEG plus ABA treatment.

Plants under drought stress produce abundantly different kind of reactive oxygen species (ROS). Increased ROS accumulation under drought stress led to damage to membranes, DNA, and proteins. On the other hand, over accumulation of ROS is kept under control by antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), peroxidase, etc. [97]. Antioxidant enzymes protect plants against oxidative stress damages by scavenging of ROS. Pre-soaking seed treatment with ABA was reported significantly enhance the antioxidant enzymes activity in wheat seedlings subjected to water stress [98]. The effects of exogenously applied ABA (10^{-6} mol/L) and drought stress imposed during tillering was compared in drought susceptible and tolerant wheat cultivars. ABA significantly increased the activities of SOD and POD. The drought tolerant wheat cultivar was found to possess higher antioxidant enzymes activity to scavenge reactive oxygen species. The pre-sowing seed treatment with ABA (10^{-6} mol/L) solution was found to ameliorate the adverse effects of drought stress in susceptible cultivar of wheat. Positive correlation was found between endogenous ABA concentration and activities of SOD and POD.

FUTURE PERSPECTIVES

Despite the environmental barriers, a large food security in the line with the new plant breeding practices needed to be done for the areas of which were under the pressure of water stress. Plant tissues subjected to drought stress firstly tend to increase their internal ABA levels and it is claimed that releasing of this hormone triggers a key cascade for activation of regulatory factors. However, ABA signaling is a complex network, identification of every molecule in this mechanism will ensure novel insights for plant molecular biology. ABA enables certain interactions between other signal mechanisms such as drought, cold and salt stress during plant growth. Also, hormonal signaling has an importance for merging the gaps belonging to other cell networks. In particular, understanding of hormone signaling will provide an extended basis for development of drought stress (abiotic stress) tolerant crops. Moreover, understanding the interactions between signal cascades and identification of novel molecules will shed lights on new gateways for future plant molecular biology research. In the sum, the use of the data obtained from ABA signaling and wheat drought stress research is often necessary for the other related monocot crops like maize and barley which have a high agricultural importance for food, feed and energy consumption.

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