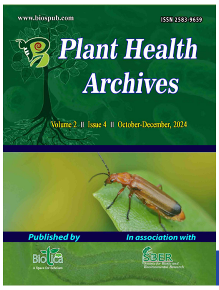

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Review Article

Role of Growth Hormones in Regulating Abiotic Stress Tolerance in Plants

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Abstract

Plants are sessile organisms and face the adverse effect of environmental changes. They regulate the adaptations to these stresses through various mechanisms. Plant hormones are important regulators that control the growth through modulation of several molecules, messengers and other signal transduction pathways under different abiotic challenges. Most importantly, the downstream metabolic processes are maintained *via* homeostasis. Current developments in molecular biology have improved comprehensive knowledge on hormonal regulation of abiotic stress. Here, we converse on the major metabolism affected by abiotic challenges mainly drought, heat, salinity and cold other than the hormonal regulation of abiotic stress tolerance. The mechanistic understanding is really crucial for the crop improvement initiatives.

Keywords: ABA, Abiotic stress, Auxin, Brassinosteroids, GA, ROS

Introduction

Environmental changes negatively impact the developmental biology in plants. Because of its sessile character, plant has developed intricate and adaptive mechanism for adapting to changing environmental signals. Consequently, both agricultural and horticulture suffer a huge crop loss (Irenaeus *et al.*, 2023). Thus, plants develop certain mechanisms in response to these external cues. Abiotic challenges appear in different forms associated with weather conditions like rainfall, temperature, irradiation, soil contaminants *etc*. Among these abiotic challenges, drought, water logging, high temperature, low temperature, salinity, heavy metals *etc*. impose major threat to plant developmental biology.

A pictorial depiction represents on how different physiological responses (Figure 1) operates for acclimatization to the external signals due to environmental stress. Plants coordinate the adaptation to various abiotic challenges through integrated action of different metabolic pathways and signalling networks to arrest the stress induced reactive oxygen species (ROS) accumulation. Plant hormones impart a crucial part in stress response through signal transduction pathways apart from its role in regulating the morphogenesis, modification and proliferation (Verma *et al.*, 2016; Salvi *et al.*, 2021). Current literature highlights the detailed function of plant hormones in regulating and ameliorating the impact of abiotic stress. In light of this,

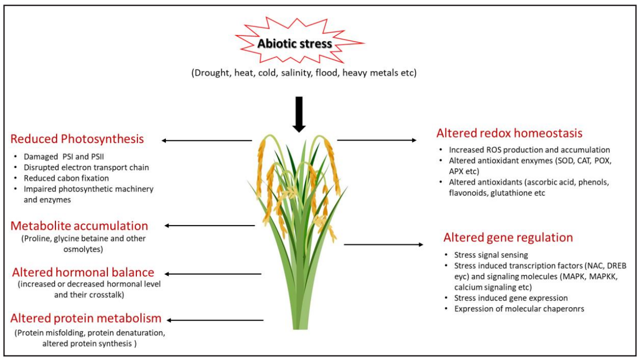

Figure 1: Plant endurance under abiotic stress

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here we addressed the significance of plant hormones in regulating the significant abiotic challenges.

Abiotic Stress and Plant Development

Under optimal conditions, plant development majorly targets to produce seeds and finishing its life cycle. However, when it encounters certain deviations like environmental changes, it has to penalize its developmental biology to ensure survival at priority that ultimately causes huge loss in crop and yield productivity. Thus, plants face the environmental changes at the expense of their growth and productivity, also known as growth trade-offs. In the process to acclimatize stress, plants activate certain tolerance mechanisms. The developmental processes are retarded under abiotic stress due to the arrest in certain major metabolic pathways. Plants face abiotic challenges starting from germination till the end of their life cycle. Water scarcity or drought during germination is itself a challenge for the plants to start its life cycle. Abiotic challenges like water limitation, salinity, high temperature *etc.* during germination reduces water potential, carbohydrate metabolism, enzymatic activity, soluble calcium and potassium ions and altered hormonal balance (Liu *et al.*, 2018). During unfavourable circumstances, the beginning of plant life cycle is largely coordinated by two major hormones *viz.* gibberellins (GA) and abscissic acid (ABA) along with other hormones. Abiotic challenges induce series of physio-morpho-biochemical modifications that alters metabolism and nutrient acquisition leading inhibition of plant growth followed by crop yield and quality loss. Although abiotic challenges arrest the cellular metabolism, photosynthetic apparatus and the redox status of the plants are adversely affected impairing plant developmental biology.

The photosynthetic machinery especially the reaction centres, PSI (Photosystem I) and PS II (Photosystem II), reaction mediated by these photosystems and chlorophyll biosynthesis are severely inhibited by abiotic challenges. On the downstream the carbon metabolism and its transport is also severely affected that in turn impairs the productivity of the plant. The major components of photosynthetic machinery are also the origin of ROS which irreparably gets damaged due to incidence of abiotic challenges. Abiotic stress causes the ROS formation disrupting PSI and PSII, which ultimately affects the light harvesting complex (LHC) (Dietzel *et al.*, 2008; Vainonen *et al.*, 2008; Pesaresi *et al.*, 2009). The inhibition of D1 protein is observed under salinity stress, chilling stress and high-light stress (Allakhverdiev *et al.*, 2002; Yang *et al.*, 2018). Non-photochemical quenching is an indispensable way to convert excessive excitation energy into heat during the light reaction. The xanthophyll cycle assists in non-photochemical quenching by detoxifying the ROS generated in the plants during heat stress, drought and salt stress (Kumar *et al.*, 2020). Besides, the crosstalk of phytohormones is important for regulation of photooxidative protection of chloroplast during stress. Furthermore, hormones like GA, jasmonic acid (JA), cytokinins and strigolactones play regulatory role in photosynthesis. GA and cytokinin has been found to improve PSI and PSII activities and strigolactones regulate the LHC (Chauhan *et al.*, 2023). Research conducted by Dobrikova *et al.* (2014) reported that brassinosteroids (BR) regulate major metabolic pathways related to LHC.

The major metabolic pathways required for plant development leads to ROS accumulation in specific organelles such as plastids, peroxisomes, apoplast and mitochondria (Rodríguez-Serrano *et al.*, 2016). These are metabolic by-products produced in usual conditions. However, their level increases as the plants are encountered to abiotic stress conditions. Under stress, ROS are the by-products of disrupted metabolic pathways as well as the part of mechanisms of signal transduction responding to abiotic stress (Choudhury *et al.*, 2017). Both these ROS alters the redox status of regulatory proteins, translation and transcription factors as response to stress. However, the stress ROS as signalling molecule sets the signal transduction that would supress the metabolic ROS generation as an acclimation response (Choudhury *et al.*, 2017). The ROS generated in chloroplast like singlet oxygen and superoxide radicle acts as signal molecule to initiate acclimation response such as chlorophyll catabolism, degeneration of photosynthetic apparatus, chlorosis, programmed cell death *etc.* by modulating the nuclear gene expression (Wagner *et al.*, 2004). Similarly, mitochondrial ROS production is mediated through the electron transport system under abiotic stress. The peroxisomal ROS accumulation is the result of photorespiration and apoplastic ROS generation is linked to various mechanisms. Therefore, the production of compartmentalized ROS modulates the redox state and alters the nuclear gene expression thereby leading to downstream change in metabolism and morpho-physiological stress response. The ROS generation or redox state of each compartment as well as the steady state level of ROS produces a typical ROS signature which varies for different abiotic challenges. Stress signalling in plants leads to increased ROS production inducing the antioxidant machinery in plants. These enzymes either act in coordination or on individual to accentuate the accumulation of ROS. Important antioxidant enzymes modulate gene expression in reaction to rising ROS levels. Mishra *et al.* (2023) discussed the increase and decrease in ROS accumulation under abiotic stress conditions along with their mechanism of action. Roy *et al.* (2017) in wheat, Sharma *et al.* (2018) in rice and Sharma *et al.* (2024) in jute have demonstrated the function of antioxidant enzymes under high temperature and drought stress. Non-enzymatic enzymes as phenols, flavonoids, ascorbic acid, glutathione, tocopherols contribute significantly in abiotic stress tolerance. Ascorbic acid being highly water soluble, antioxidant plays crucial role in signalling pathway (Roy *et al.*, 2023; Mishra *et al.*, 2023; Sharma *et al.*, 2024). By scavenging free radicals and regenerating tocopherol from the tocopheroxy radical, it helps to preserve membranes significantly. Tocopherol, particularly α-tocopherol is essential in mitigating potoxidative damage by quenching singlet oxygen. Similarly, glutathione, a tripeptide antioxidant found predominantly in chloroplast, eliminates ROS along with ascorbic acid and NADPH through

Halliwell-Asada Pathway (Bagheri *et al.*, 2017). Researchers have demonstrated the function of carotenoids as key antioxidants, quenching singlet oxygen and neutralizing free radicals such as peroxy ($ROO^{\bullet}$), Hydroxy ($^{\bullet}OH$) an superoxide ($O_2^{\bullet -}$) thereby protecting plants under abiotic stress conditions.

ROS and hormonal interplay control the morphgenesis and growth of plant. However, the ROS which were once thought to be toxic molecules are now considered as special signal molecules allowing plants to adapt stress conditions through calcium dependent pathways, MAPKK pathways and other hormonal pathways. A study showed that mutants with suppressed ROS signalling showed alleviated stress indications (Suzuki *et al.*, 2013). The reduction in stomatal closure caused by ABA induced ROS generation through calcium signalling under drought was associated with the decrease in the level of hydrogen peroxide (H_2O_2) content (Mignolet-Spruyt *et al.*, 2016). Under Cadmium stress, the H_2O_2 content affected the auxin distribution including transport, biosynthesis and signalling in rice stating that auxin acts upstream to auxin signalling in rice (Zhao *et al.*, 2012). Conversely, brassinosteroids (BR) promote ROS production in plants and these induce tolerance by enhancing the build-up of ROS especially H_2O_2. This, in principle, initiates H_2O_2 mediated signalling cascade interceding stress tolerance through increase in stress regulated genes and transcription factors like dehydrins, antioxidants, heat shock proteins (HSPs) *etc.* (Jiang *et al.*, 2012). To conclude, redox signalling serves as key indicator and regulates stress tolerance ultimately altering the plant developmental biology.

Role of Plant Hormones

Under abiotic stress, the hormonal homeostasis is reprogrammed to signal the primary metabolism of the plants according to different stress conditions (Table 1). These hormones regulate developmental biology amongst the trade-offs during stress tolerance. To carry out the proper functioning of the metabolic pathways, the plant signal transduction turns on and optimizes the ratio of hormonal content, distribution and crosstalk in such a way that the plants perform at its best in the prevailing environmental conditions. In this segment we talk about the crosstalk of hormone under different conditions.

Drought Stress

Drought and climate change, in the context of agriculture and horticulture, is responsible for 20-30% of global yield loss but in extreme cases, it can exceed to 50% in all over the world. Thus, targeting the kind of the physiological response at the cellular level will ensure better amelioration strategies for engineering drought tolerance in crop species. One of the key signalling molecules is the abscisic acid (ABA) which has been thoroughly explored for drought response in many species. Metabolics, genomics transcriptomics profiling of plants under drought suggested the function of ABA responsive genes and accumulation of typical metabolites including proline in *Arabidopsis* under drought. This was accompanied by decrease in amino acids content, alteration in ethylene and GA signalling (Skirycz *et al.*, 2011). ABA dependent transcriptional regulation degraded leaf starch content to increase the sugar required for osmotic adjustment (Thalmann *et al.*, 2016). The dynamic alteration

Table 1: Role of hormone in regulating plant growth

Hormones	Aberration	Effect	References
Auxin	Relocation of PIN3 auxin transporters to the lower sides of the same cells	Redirect the auxin flow to this side of the root, causing differential auxin distribution, asymmetric growth and ultimately downward bending of the root.	Friml *et al.*, 2002
Gibberellin	Loss-of-function mutation in four genes (SbCPS1, SbKS1, SbKO1, SbKAO1) involved in the early steps of GA biosynthesis	Severe dwarfism but also in abnormal culm bending.	Ordonio *et al*., 2014
Cytokinin	Stacking one, two and three of the genes encoding a subfamily of histidine kinases (CRE1, AHK2 and AHK3) that function as cytokinin receptors	Including inhibition of root elongation, inhibition of root formation, cell proliferation in and greening of calli and induction of cytokinin primary-response genes.	Higuchi *et al*., 2004
ABA	Reduced abscisic acid (ABA) production (*sitiens*)	Increased cuticle permeability, which is positively correlated with disease resistance. Furthermore, perturbation of ABA levels affects pectin composition.	Curvers *et al*., 2010
Melatonin	Silenced SlCOMT1 gene expression	Decrease in the individual fruit weight, seed number per fruit.	He *et al*., 2023
Brassinosteroid	BR insensitive mutants	Compact rosette structure, decreased plant height and reduced root system, delayed development and reduced fertility.	Schröder *et al*., 2014

in ABA responsive manner is evident under drought (Heinemann *et al.*, 2021). Cysteine and tryptophan plays a vital role in regulating ABA mediated signalling (Batool *et al.*, 2018; Chen *et al.*, 2019; Liu *et al.*, 2022; Soda *et al.*, 2022). A study showed that increase in sulfate level in root xylem sap of maize under drought condition regulated the stomatal opening and closure. The sulphur content in the xylem sap controls the availability of cysteine and tryptophan which consequently alters the guard cells controlling the stomatal opening under drought (Batool *et al.*, 2018).

Furthermore, other hormones' interaction with ABA regulates plant growth through alteration by transcriptional and post translational mechanism under drought. Hormones affecting developmental biology and additionally play a crucial role in abiotic stress tolerance. Auxin in coordination with ABA regulates the directional growth of root towards moisture primarily driven by auxin pathway (Taniguchi *et al.*, 2010; Xu *et al.*, 2013). Furthermore, drought stress affects auxin biosynthesis, auxin transport and auxin signal transduction pathway. Several studies have reported that major auxin biosynthesis genes alleviate drought impact in many crops. Auxin applied exogenously has been shown to upregulate the ABA promoters in *Arabidopsis* and soybean (Lee *et al.*, 2012; Kim *et al.*, 2013; Park *et al.*, 2019).

This clearly depicts the association of ABA with auxin in growth trade-offs under stress (Shi *et al.*, 2014). The ameliorative effects of exogenous auxin application were observed on white clover and rice under drought tolerance (Sharma *et al.*, 2018; Zhang *et al.*, 2020). Drought tolerance was reduced by loss of function mutants in auxin signalling genes such as *IAA5*, *IAA6* and *IAA19*, which are again linked to ABA-regulated genes (Salehin *et al.*, 2019). Auxin mainly controls the drought stress by regulating the ROS along with ABA. Thus, a better understanding of the crosstalk is essential to find insights into developmental biology under drought.

Drought further reduces GA accumulation, biosynthesis, signalling, water use efficiency and cell membrane stability (Wang *et al.*, 2008). The GA biosynthetic genes in susceptible soybean cultivar compared to the tolerant showed down regulation suggesting that GA has major function in conferring drought tolerance (Bashir *et al.*, 2019). The alteration of root elongation (lateral) and reduction of GA2-oxidases under drought is a crosstalk of GA and IAA (Chen *et al.*, 2019). Under stress conditions, GA2-oxidases (GA2ox), along with DELLA domain proteins such as GAI (GA Insensitive) and RGL1 (Repressor of GA1-3 Like), play key roles in GA biosynthesis and signalling. GA2ox enzymes induce dwarfism by inhibiting bioactive GAs (Lo *et al.*, 2017; Rieu *et al.*, 2008). Further the DELLA domain proteins, the stress survivors (Achard *et al.*, 2007; Zhou and Underhill, 2017), functions by suppressing cellular activity (Olszewski *et al.*, 2010; Claeys *et al.*, 2012). High cytokinins, related to delayed senescence and source sink associations, have important relation with photosynthesis and stress regulation. The over expression of rate limiting cytokinin biosynthesis gene *IPT* (*ISOPENTENYL TRANSFERASE*) and related promoters shows delayed leaf senescence, delayed flowering (Ma, 2008) resulting in alleviated drought stress response. *IPT* gene expression accompanied with a maturation- and stress-inducible *SARK* promoter increased the cytokinin level in monocots and dicots (Rivero *et al.*, 2007; Peleg and Blumwald, 2011; Qin *et al.*, 2011). Developed transgenic rice and tobacco exhibited modifications in hormonal synthesis and regulatory pathway, leading to altered photosynthesis and source-sink relationship, ultimately enhancing yield under water stressed condition (Peleg and Blumwald, 2011); (1-aminocyclopropane-1-carboxylate) under osmotic stress are known to arrest (Skirycz *et al.*, 2011) through *ERF*/*AP2* transcription factors resulting in reduced cell proliferation activities. Studies show that *ERF5* and *ERF6* deactivate GA *via GA2ox6* inhibiting leaf proliferation and cell activity (Dubois *et al.*, 2013). GA levels in response to ACC levels modulate ERF transcription factors increases further on exposure to drought stress. Further BR also regulates the drought stress metabolism. However, an antagonist relationship exists between these two hormones. For example, RD26 (Responsive to Dessication 26), a NAC transcription component, positively regulates ABA-responsive genes (Fujita *et al.*, 2004) while it is negatively regulated by *BES1* (*BRI1-EMS-SUPPRESSOR 1*), a transcription factor in BR signalling pathway (Yu *et al.*, 2011). It was further found out that drought induced ABA signalling or BR growth signalling was turned on or off by the transcriptional repression and protein-protein interaction of *RD26* and *BES1* (Ye *et al.*, 2017). Moreover, the interaction of other hormones with ABA, such as salicylic acid, jasmonic acid, strigolactones, melatonin and polyamines, remain important to mediate stress tolerance. While change in the endogenous level of ABA is the first response as the roots sense moisture deficit, the acclimation to drought and the growth trade to maintain survival is the crosstalk of all hormones and the metabolic pathways.

High Temperature

High temperature is one of the rising concerns of global warming and imposes heat stress on plants that further alters the plant developmental biology (Ding *et al.*, 2020). High temperature induces physio-biochemial changes that affect molecular mechanism resulting in morphological changes in crop developmental biology. It causes protein misfolding and generation of ROS which are toxic to the plants. These misfolded proteins must be degraded and ROS must be scavenged to impart heat stress tolerance. Thus, plant activates the heat stress responsive genes that encode the chaperones and ROS scavengers. Among these, heat shock factors (HSFs) and heat shock proteins (HSPs) are master regulators that confer thermotolerance to plants (Ohama *et al.*, 2017). The misfolded proteins in rice and *Arabidopsis* under heat stress have been highlighted to be renatured by HSF encoded HSPs (Kotak *et al.*, 2007). Other transcription factors like *bZIP* and *NAC* are concerned in the removal of misfolded proteins and the high temperature activated antioxidant enzymes removes the ROS (Ding *et al.*, 2020). Apart from these, plant hormones mediated response and signal transduction is one of the effective systems for detecting and responding to elevated temperatures. A heat induced morphological phenomenon known as thermomorphogenesis is one of the crucial responses of auxin under increased temperature (Casal and Balasubramanian, 2019). *PIF4* (*PHYTOCHROME INTERACTING FACTOR 4*), known for regulating photomorphogenesis, also regulates thermo-morphogenesis at higher temperature by regulating the auxin biosynthesis in *Arabidopsis*. The auxin biosynthesis mutant, *yuc8,* showing a reduced hypocotyl elongation confirms the interaction of PIF4 with auxin in the regulation of the stem growth (Sun *et al.*, 2012). Further auxin transport also affects Thermo-morphogenesis. The polar auxin transport inhibitor NPA (1-naphthylphthalamic acid) has been shown to impede thermal responsiveness under high temperature (Stavang *et al.*, 2009). Besides auxin, gibberellins (GA) and brassinosteroids (BR) also significantly contribute to thermomorphogenesis. The transcript level of GA biosynthesis genes like *AtGA20ox1* and *AtGA3ox1* are increased in hypocotyl at slightly high temperatures to regulate cellular proliferation (Stavang *et al.*, 2009). Again, under high temperature the hypocotyl elongation was observed with the breakdown of DELLA proteins *RGA* at the hypocotyl zone. The interaction of DELLA proteins with PIF4, BZR1 (Brassinazole-Resistant 1; a transcription factor in BR signalling) and ARF8 (Auxin Response Factor 8; a transcription factor in auxin signalling) performs a vital function in modulating cell elongation (de Lucas *et al.*, 2008; Feng *et al.*, 2008; Bai *et al.*, 2012; Oh *et al.*, 2014). To further understand in depth, genetic and pharmacological studies was conducted and the results showed that for thermomorphogenesis response BR acted downstream to auxin and GA (Stavang *et al.*, 2009; Ibanez *et al.*, 2022). For instance, the elevated temperature induced root growth is the BR mediated response rather than primary function of auxin and other factors involved in root development through the disruption of BR signalling pathway (Martins *et al.*, 2017). Thus, thermomorphogenesis is a response coordinated by crosstalk of auxin, GA and BR.

Auxin also plays a crucial role in pollen development and it was found that reduction in auxin content and biosynthesis under high temperature was associated with male fertility in barley and rice (Sakata *et al.*, 2010; Sharma *et al.*, 2018). Not only the endogenous auxin content and biosynthesis but the signalling is also impaired under high temperature stress. The *arf17* knockout mutant, an auxin signalling mutant, showed disrupted male fertility with increased callose deposition around the pollen tetrad (Yang *et al.*, 2013). Thus, auxin is a fundamental regulator of male fertility and pollen development under elevated temperatures, mediated by its production, transport and signalling. Additionally, the exogenous IAA (Indole-3-acetic acid) or auxin application of under drought and heat condition improved the pollen viability, male fertility and yield of barley and rice (Sakata *et al.*, 2010; Sharma *et al.*, 2018). High temperatures reduce GA biosynthesis by downregulating GA20ox and GA3ox genes, while simultaneously enhancing ABA biosynthesis through the upregulation of ABA1/ZEP (Zeaxanthin Epoxidase) and NCED (Nine-cis-Epoxycarotenoid Dioxygenase 2) transcripts. The reduction in endogenous GA in seeds thus activated *SPY* (*SPINDLY*, an O-GlNAc transferase) and inhibits germination at higher temperatures (Toh *et al.*, 2008). Jasmonic acid has recently emerged as a significant regulator of heat stress. An increase in jasmonate content was noticed in *Arabidopsis* when exposed to high temperature (Clarke *et al.*, 2009) whereas others found it to be reduced (Du *et al.*, 2013). Consequently, JA signalling was also affected on exposure to heat stress (Sharma *et al.*, 2016). Research indicates that gibberellin biosynthesis genes as *GA20ox* and *GA3ox* are promoted under heat stress *via* increased levels of melatonin content. Melatonin mitigates H_2O_2 accumulation by stimulating antioxidant enzyme action (Marta *et al.*, 2016; Wang *et al.*, 2022). Furthermore, salicylic acid regulates the membrane stability under heat stress by modulating the actions of antioxidant enzymes. The exogenous salicylic acid was found to ameliorate the negative impact of thermal stress in tomato and *Medicago* (Jahan *et al.*, 2019; Wassie *et al.*, 2020). Although both salicylic acid and jasmonic acid are known for defense response against biotic stresses, their role in abiotic challenges is emerging. Heat stresses have diverse morphological response but all are mediated through generation of ROS and plant hormones mostly modulate the redox status and ROS homeostasis through efficient mechanisms to enhance the thermal tolerance in plants.

Salinity Stress

Soil salinity has been a threat worldwide and has increased drastically to pose a global threat on agricultural yield (Zandalinas *et al.*, 2021) due to increase in temperature and the consequent water scarcity resulting in salt accumulation (Gamalero and Glick, 2022). Plant developmental biology is impaired under salinity conditions (Mustapha *et al.*, 2024). With the change in the soil pH due to accumulation of ions such as Na^+, Mg^{2+}, Ca^{2+}, Cl^-, SO_4^{2-}, Cl^-, HCO_3^-, the root development is affected at the first instance. Salt stress accompanies uptake of toxic ions. Consequently, the reduced uptake of water results in water deficit, ion imbalance and ion toxicity. The dry biomass of plants is severely reduced attributable to the decrease in shoot and root growth most likely due to the impairment in cell wall biosynthesis. The continuous uptake and accumulation of ions like Na^+ increases competition for the essential element like K^+ which leads to K^+ deficiency and lower K^+/Na^+ ratio in the plants thereby leading to a series of physiological and biochemical changes like reduction in chlorophyll and protein content, increase in stress metabolite and ROS accumulation and alteration in antioxidant machinery (Aizaz *et al.*, 2024). To combat this effect, plants employ different mechanisms like ion exclusion, modification at the root zone, ion accumulation in vacuole, alteration in signal transduction through transcription factors or hormonal network. Plant hormones regulate the plant metabolism under salt stress through osmoregulation, redox and ionic homeostasis, along with their crosstalk with major transcription factors (Xiao and Zhou, 2023). Salt stress responses are mainly triggered by excess accumulation of Na$^+$, changes in intracellular Ca^{2+} levels and ROS generation (Zhao *et al.*, 2021).

As a key regulator of osmotic stress, ABA plays an important role in the salt stress response. Salinity increases endogenous ABA levels, subsequently activates SnRKs (Sucrose Non-Fermenting-1 Related Kinase-1). SnRKs further phosphorylate AREB/ABF (ABA-Responsive Element-Binding Protein/ABRE-Binding Factor) transcription components, leading to the regulation of stomatal closure under osmotic stress (Cai *et al.*, 2017). Salt stress subsequently increases the calcium ion concentration in the cytosol that imbalances the ion equilibrium state. However, under salt stress, the Ca^{2+} ions are restricted for release and accumulate in the roots. ABA assists in releasing these Ca^{2+} ions from the intracellular storage by signalling the activation of plasma membrane-bound channels (Edel and Kudla, 2016). To maintain the ion balance between Na$^+$ and K$^+$, K$^+$ uptake is balanced with ABA-SnRK2.6-activated potassium channel *KAT1* and Ca^{2+}-CBL1/9-CIPK23 signalling module-activated *AKT1* (K$^+$ TRANSPORTER 1) *Arabidopsis* that causes the reduction Na$^+$:K$^+$ ratio (Yang and Guo, 2018). In addition to ABA, ethylene is also thought to be a master regulator of plants response to salinity. Increase in ethylene and its precursor ACC is linked with salt stress (Gieniec *et al.*, 2024). Salinity tolerance of ACC treated *Arabidopsis* plants showed enhanced salinity tolerance at different developmental stages (Cao *et al.*, 2007). Moreover, upregulation of ethylene biosynthesis anf its content was found in *eto1* and *eto2* mutants under salinity stress (Jiang *et al.*, 2013). Ethylene signalling is also important in addition to ethylene biosynthesis under salt stress. Studies conducted by Cao *et al.* (2007), Jiang *et al.* (2013) and Wilson *et al.* (2014) found that enhanced salinity tolerance is a result of loss in function of ethylene receptor. Interestingly, *etr1* different phenotypes depicting their crosstalk in providing salt stress tolerance. This confirms that ABA-ethylene crosstalk is a key regulator of salt tolerance in plants (Wilson *et al.*, 2014). ABA under salt stress also induces the cytokinin and strigolactone mediated plant response. Strigolactone mediated signal transduction is increased under salt-stress conditions. The reduction in cytokinin and therefore, the increase the sensitivity of the plants to ABA under salt stress is reported (Yu *et al.*, 2020). Further the auxin biosynthesis also seems to be boosted up under salinity stress. The auxin biosynthesis genes (NIT1, NIT2 and YUC4) were upregulated followed by NaCl treatment in *Arabidopsis* (Cackett *et al.*, 2022). Studies by Liu *et al.* (2015) and Fu *et al.* (2019) have highlighted the role of *PIN1, PIN3 PIN 7* in auxin transport and salt stress disrupts the expression of the genes. Interestingly, the expression of certain auxin biosynthesis genes has increased in *Cucumus sativus* and potato (Kim *et al.*, 2013; Yan *et al.*, 2016) under salt stress. *PIN1* also plays important function in the growth of plant epidermal cells under drought and salt stress conditions (Bawa *et al.*, 2022). Similar to auxin transport, the auxin signalling is also inhibited that further impairs the auxin mediated response under salt stress. The auxin receptors TIR1 (TRANSPORT INHIBITOR RESPONSE 1) and AFB2 (AUXIN-SIGNALLING F-BOX 2) were downregulated under salt stress, indicating a growth trade-off (Iglesias *et al.*, 2014; Yu *et al.*, 2020). The hormones thus mediate the morphological, physiological and biochemical response to salt stress by transforming their biosynthesis, transport, signalling and their cross talk.

Cold Stress

Cold stress greatly affects the plants growth, productivity and survival, while also restricting the geographical distribution of species (Uemura *et al.*, 1995; Kidokoro *et al.*, 2022). The plant's exposure to temperature range of 0-15 °C imposes chilling stress while below that of 0 °C imposes freezing stress. This results in a sequence of physiological changes in plants such as membrane damage, ion leakage, altered redox homeostasis, reduced water uptake, osmotic stress, inter- and intra-cellular ice crystal formation, protein destabilization and denaturation, loss of chlorophyll and photosynthetic activity, retarded plant developmental biology that ultimately results to lower yield. However, the plants adapted to environment with lower temperatures have evolved mechanisms called as the cold acclimation to manage its survival. One of the responses involves mobilization of reserves from photosynthetic organs to storage tissue (Thorsen and Höglind, 2010). Further the cold hardening is the physiological response that allows these plants to endure the subzero temperature (Song *et al.*, 2012). The low temperature signal is sensed by the plants that initiate the signal transduction cascade to alter the gene expression required to adapt to cold temperatures. Studies show that plants that are adapted to freezing tolerance can adapt upto -30 °C while the non-acclimated plants can tolerate upto -5 °C (Raza *et al.*, 2023). Moreover, the tropical crops like maize (*Zea mays* L.) and tomato (*Solanum lycopersicum* L.) are unable to tolerate freezing (McKhann *et al.*, 2008). Plant hormone plays important to in adapting to cold stress like any other abiotic stress. The major target of plants' responses to cold stress is increasing the membrane fluidity, stabilization of protein structure and maintains the redox homeostasis to maintain the primary metabolism for growth and survival. However, the phenotypic response of cold acclimated plants differs from the non-acclimatized plants and depends on the intensity of cold exposure. It includes chlorosis, reduction in leaf expansion, necrosis and reduced biomass (Enders *et al.*, 2019). At the gene regulation level, cold stress primarily triggers the ICE1-CBF-COR transcriptional cascade, where ICE1 (Inducer of CBF Expression) activates CBFs/DREBs (C-repeat Binding Factors/Dehydration-Responsive Element Binding Protein). In turn, these bind to the promoters of COR (Cold-Regulated) genes, initiating their transcription and enabling cold stress adaptation (Shi *et al.*, 2015; Ding *et al.*, 2019; Yang, 2022). As in case of any other stress, ABA plays a crucial role here. The exposure of cold increases the endogenous ABA content that acts as intracellular signal to maintain the protein synthesis. Further, the transcription of genes for antioxidant enzymes has been reported to be increased by exogenous ABA, which in turn enhances cold stress tolerance in large numbers of plants (Qin *et al.*, 2019) by enhancing the activities of POX, CAT, SOD, APX and GR, the accumulation of H_2O_2 in wheat is reduced, even under extreme temperatures ranging from 0 °C to -24 °C (Yu *et al.*, 2020). ABA interacts with polyamines to induce cold stress tolerance in rice (Zheng *et al.*, 2023). Likewise, BRs also regulate the membrane fluidity, maintains redox levels by regulating the activities of antioxidant enzymes, photosynthetic activities under cold stress. BRs play a pivotal role in maintaining membrane fluidity under stress. Due to its similar structure to plasma membrane, the BRs maintain the plasma membrane flexibility in surface structure (Filek *et al.*, 2017). Kim *et al.* (2013) and García-Pastor *et al.* (2020) reported certain mutants of Brassinosteroids which showed enhanced cold tolerance by upregulating the expression of ABA receptors which resulted in reduced membrane injury altering fatty acid profile and enhancing antioxidant enzymes. Studies show that extreme cold stress increased levels of auxin, cytokinin and salicylic acid level and decreased jasmonic acid and ABA levels in wheat (Wang *et al.*, 2024). Moreover, the transcriptomic and metabolic profiling have suggested a number of genes, metabolites and biochemical pathways to be modulated under cold stress. For example, cold stress positively integrates ABA signal transduction and sugar metabolism pathways improve the cold stress tolerance of *Argyranthemum frutescens* (Xu *et al.*, 2023). Thus, the omics approaches when integrated with gene manipulations have high potential to provide insights into phytohormone associated pathways and their role in cold stress.

Growth hormones are thus important and integral part of stress signal transduction pathway. Moreover, literature has evidences that exogenous application of these hormones also regulates the stress mediated response (Table 2). Most of these exogenous applications of hormones have ameliorative effect on stress. These function mostly through quenching of ROS and enhancing the antioxidant machinery using vital signal transduction pathways as well as modulating their biosynthesis, transport and signalling under stress. The protecting effect of these hormones thus may be exploited at larger scale to alleviate the negative consequences of climate change.

Table 2: Exogenous application of different hormones and their effect on plants

Plant Hormone	Species/ Crops	Stress	Response	References
Auxin	Rice	Drought	Exogenous auxin and genetic manipulation of auxin synthesis and signalling will be useful to mitigate spikelet sterility and stabilize the grain yield of rice under drought and heat stresses.	Sharma *et al*., 2018
	Zea mays L.	Salt stress	IAA mitigated the adverse effects of salinity on maize plants. The most promising effect of IAA or K and P on alleviation of salt stress on maize was found when they were applied in combination.	Kaya *et al*., 2013
Gibberellic Acid	Wheat seeds	Salt stress	A positive result on germination in salinity conditions was found after priming of wheat seeds with GA3.	Abido *et al*., 2019
Cytokinin	Maize	Drought	Maize foliar spraying with cytokinin solution at different concentrations in vegetative phase of development was very effective in alleviating drought-imposed adverse effects whereas cytokinin had very little effect at the reproductive phase.	Akter *et al*., 2014
	Rice	Drought	Exogenous spraying of rice plants at tillering and grain-filling stages with synthetic cytokinin phenyl urea improved the stomatal conductance of leaves, which was reduced by drought.	Gujjar *et al*., 2020
ABA	*Zea mays* L.	Drought	Foliar treatment with ABA increased drought tolerance in young corn plants and induced the accumulation of glycine betaine, enhanced water content and dry biomass.	Zhang *et al*., 2012
	Wheat grains	Drought	ABA priming of wheat grains induced drought tolerance, increased soluble proteins content and productivity.	Khan *et al*., 2012
	Elymus nutans	Cold tolerance	Melatonin induction of antioxidant protection was realized through the ABA-dependent signalling pathway.	Fu *et al*., 2017

Plant Hormone	Species/ Crops	Stress	Response	References
Salicylic acid	Rice	Cadmium stress	Treatment of rice with SA in low and high concentration had a positive effect on metabolism, developmental biology of plants, both in control and stress conditions.	Mostofa *et al*., 2019
	Maize	Salt stress	SA foliar treatment under salt stress improved the yield, increased an antioxidant protection and stabilized the photosynthetic activity of corn.	Tahjib-Ul-Arif *et al*., 2018
Brassinosteroids	Rice	Metal stress	After foliar treatment with BSs, the toxic effect of heavy metals in rice was reduced and partially limited; an increase in photosynthetic pigments content, promoted photosynthesis, dry biomass accumulation, decreased H2O2 content and increased antioxidant enzyme activity was found.	Sharma *et al*., 2016
Melatonin	Maize	Cadmium stress	The effects of exogenous melatonin and N application on maize under Cd stress revealed notable enhancements in root length, volume and biomass, alongside a reduction in Cd accumulation.	Ma *et al*., 2021
	Barley	Polymetallic stress toxicity	Exogenous melatonin reduces polymetallic stress toxicity in barley, by modulating circadian genes, regulating rhizosphere microbial communities and boosting antioxidant activity, serving as key defensive mechanisms.	Jiang *et al*., 2022
	Cotton	Drought	Melatonin application significantly improved the translocation of carbon assimilates to drought-stressed anthers.	Hu *et al*., 2020
Jasmonic Acid	Soybean	Salinity	Increased root fresh and dry weights, chlorophyll content, photosynthesis rate and transpiration rate.	Yoon *et al*., 2009
	Wheat	Drought	Increased grain, biological yield and wheat adaptability.	Anjum *et al*., 2016
	Brassica napus	Heavy metal toxicity	Enhanced antioxidant defence system, secondary metabolite and reduced arsenic contents.	Farooq *et al*., 2016

Conclusion

To survive in abiotic stress conditions, plants implement a range of biochemical, morphological, physiological and cellular adaptations. The regulation of stress-mediated response is significantly influenced by plant hormones, particularly ABA. In most of the cases, it regulates responses by interacting with other hormones. Controlling primary metabolism depends much on the interaction of hormones, transcription factors and the signal transduction system. Understanding these intricate relationships will help us to better know hormonal control in plant development under stressful circumstances. Genetic engineering and genome editing tools help to create climate-smart varieties even more by means of this understanding. On the mitigation front, plant hormones have been studied for their exogenous application to minimize stress-induced damage, with potential for large-scale commercial use. However, clear understanding the hormonal regulation under abiotic stress requires more efforts for crop improvement program and enhances agricultural productivity.

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