

Role of Plant Hormones Under Abiotic Stress Conditions

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Abstract:

Plants are continuously subjected to various environmental signals (Abiotic stress conditions) like nutrient supply fluctuations, dryness, temperature, freezing, excessive salt, or heavy metal, all of which can negatively impact their development, survival, etc., and viability. Reducing agricultural losses and generating more food products to meet the demands of humans have become increasingly important. Phytohormones portray plants' capability to acclimatize them to environmental conditions by modulating development, nutrient distribution, and source/sink transitions. Phytohormones, like auxins, cytokinins, ethylene, gibberellins, brassinosteroids, jasmonates, and strigolactones, have recently been crucial metabolic candidates for developing abiotic resistance in crops and have a regulatory role in plant adaptability and defense operations. Hormones travel via specialized paths to regulatory areas, where they react to stress with deficient levels. Mechanisms underlying biochemical, molecular, genetic, and physiological concepts of plant hormones that underpin plant adaption and defensive tactics represent a substantial cognitive foundation for developing innovative plant biotechnology. The crosstalk between phytohormones causes synergetic or antagonistic relationships that are important in plants' response to abiotic stress. The current article evaluates plant hormones' role in plant survival and growth under abiotic stress tolerance conditions.

Keywords: abiotic stress, phytohormones, agricultural losses, synergetic, antagonism.

Highlights:

- Abiotic stresses are being detrimental to agricultural production
- Phytohormones are being used for modifying physiological and molecular responses of the plant under abiotic stressors
- Cytokinin and Brassinosteroids are being used to mitigate the stresses

1. INTRODUCTION:

The world's population is quickly growing, necessitating a significant rise in agricultural production. Plants have a distinct and more complicated environmental stress response and tolerance mechanisms than animals (Qin *et al.*, 2011). Identifying those mechanisms is one of the crucial aspects of high production. For crops, abiotic variables seem to be the most critical yield-limiting constraints (Canter, 2018; Zörb *et al.*, 2019). The abiotic stressors like high or low temperature, salinity, heavy metals, or drought might affect nearly all physiological and biochemical, including molecular processes in plants, from seed to maturity. They can have a detrimental effect on the economic output of diverse agricultural plants. These activities or mechanisms are regulated by plant growth regulators (plant hormones), substances produced from plant biosynthetic pathways that could operate either at the site of synthesizing or after their transit elsewhere in the plant.

Phytohormones are the organic constituents produced within the plant and arise in low concentrations that regulate the various cellular processes in plants. Plant growth regulators or phytohormones or plant hormones include auxin, cytokinins (CK), gibberellins (GA), ethylene (ET), abscisic acid (ABA), jasmonates (JA), brassinosteroids (BR) and salicylic acid (SA). Therefore it's conceivable that more growth regulators may be identified. Those are biodegradable and greatly enhance crop growth and output in both ideal and stressful events. Phytohormones act as chemical messengers which regulate cell functions in cellular compartments locally and yet when they travel to other regions of the plant.

Phytohormones are essential in the abiotic stress response (Fig. 1), coordinating numerous signal transduction pathways. They are in charge of both external and interior stimuli (Kazan, 2015). Auxin, cytokinins, gibberellins, and brassinosteroids help regulate plant growth and development, while ABA is considered a stress hormone, whereas salicylic acid, ethylene, and jasmonates have a significant impact on regulating the immunological responses in plants. Moreover, phytohormones are linked with the complex network to balance the responses to different environmental conditions. The molecular mechanisms that command these hormonal traps are unknown (Fig.1).

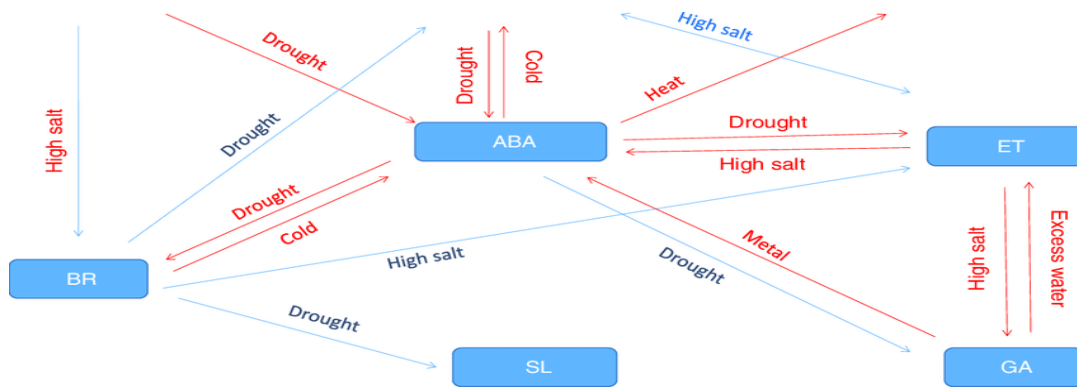


Figure 1. shows the roles of plant hormones in abiotic stress tolerance.

Specifically, conventional growth-promoting plant hormones have recently emerged as essential integrators of both plant immune and abiotic stress responses, minimizing stress-related viability losses (Denancé *et al.*, 2013; Peleg and Blumwald, 2011). Biotechnologists may be able to boost crops economically and nutritionally by using phytohormone synthesis. The relevant knowledge on plant hormone regulation of abiotic stress reactions is outlined in this review, emphasizing additional insights into the complex hormonal crosstalk of classical growth-stimulating phytohormones within the naturally occurring abiotic multi-stress atmosphere of higher plants.

2. Abiotic Stress: A Threat to Crop Yield & Performance:

Agricultural production and quality are determined mainly by genotypes, ambient conditions, and cultivating management. Extreme temperatures, drought, flooding, salt, and heavy metal stress, among other abiotic variables, have influenced plant development and crop productivity (Waqas *et al.*, 2017; Vaughan *et al.*, 2018; Zafar *et al.*, 2018). The factors reduce the yield by 50-70% and negatively influence the physiological and biochemical processes of plants. To promote stress tolerance, photosynthetic efficiency and light-use efficiency could well be controlled at the physiological level. Several antioxidant mechanisms can be triggered at the biochemical level, and many enzymes can create stress-related intermediates to prevent cellular damage.

Environmental issues are frequently identified as one of the agricultural sector's future problems (Fig. 2). Of all the factors influencing the crops is the high temperature, the most crucial variable that diminishes water quality and quantity. On the other hand, heavy rain can lead to floods in various agricultural fields, wreaking havoc on crop development and productivity. However, low temperature is also a problem for the species whose blooming period is in spring. Chilling injury or injury to flower leaves caused by cold stress can result in considerable crop loss. Inappropriate crop nutrition can result in excess or a lack of certain critical nutrients, impacting plant development, yield, or quality, depending on the species. In different agricultural and urban sectors, an overabundance of heavy metals or toxic compounds can potentially be a limiting factor. A compilation of agronomic solutions for inducing crop tolerance in the short term has been particularly outlined (Mariani and Ferrante, 2017; Ferrante and Mariani, 2018).

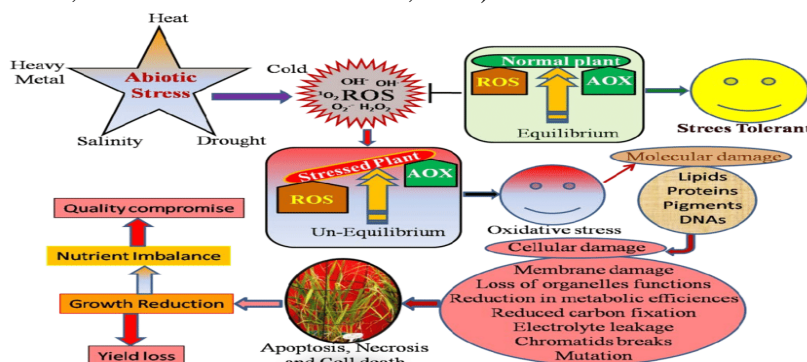


Figure 2: Abiotic stresses that can severely affect crop yield and quality.**3. Plant Hormones Regulating the Abiotic Stress:**

Phytohormones are significant endogenous chemicals for modifying physiological and molecular responses, and a necessary for crop growth, even though plant response to abiotic stressors is influenced by various circumstances (Fahad *et al.*, 2015). ABA, SA, JA, and ET are known to mediate plant defensive mechanisms against pathogens and abiotic stresses (Bari and Jones, 2009; Nakashima and Yamaguchi-Shinozaki, 2013). Drought, salt, frost, excessive heat, and injury cause ABA levels (Table 1) rise, hence why ABA is vital for plant resistance against abiotic stimulation (Lata and Prasad, 2011; Zhang *et al.*, 2006). Recent research has found that SA, JA, ET, and ABA, interact with auxins, CKs, and GAs in regulating the defense system of plants (Bari and Jones, 2009; Navarro *et al.*, 2008; Nishiyama *et al.*, 2013).

Table 1 Depicts the role of these phytohormones in evoking varied responses in various crop plants.

Plant Name	Plant hormone	Abiotic stress (type)	Resultant reaction	References
Pearl millet	ABA and JA	Drought	Exogenous use improved the chlorophyll improved plant defense mechanism due to enhanced activities of antioxidant enzymes and relative water content of seedlings, which improved their growth profile.	Awan et al., 2020
Foxtail Sophora	Auxin, CK, GA, BR, and SA	Salinity	Auxin, CK, GA, and BR are involved in growth and recovery mechanisms, and SA balances plant growth or resistance by avoiding the loss of growth-promoting hormones while keeping high levels of ABA.	Zhu et., al 2021
Tomato	JA	Salinity	JA's endogenous application by conserving plants through the activation of both enzymatic and non-enzymatic antioxidants in response to salt-induced oxidative stress.	Abouelsaad and Renault, 2018
Soya bean	GA.	Salinity	GA3 treatment increased plant height and fresh/dry biomass substantially.	Hamayun et al., 2010
Tobacco	Auxin & CK	Drought	Auxin and CKs contribute to the root response to extreme drought, including main root growth promotion and branching inhibition.	Havlova et al., 2008
Mustard greens	Methyl jasmonate	Metal stress (Cr)	Through an improved antioxidant defense mechanism, secondary metabolite, and lower arsenic levels, MJ promotes ROS scavenging.	Farooq et al., 2016
Common sage	SA.	Metal stress (Cu)	Spraying SA on stressed plants boosted stem and root growth and increased calcium, phosphorus, potassium levels, and essential oil content.	Es-sbihi et al., 2020

3.1 Cytokinin (CK) Against Abiotic Factors:

CKs are among five major groups of phytohormones that influence plant growth and development and play a significant role in the cell cycle (Hönig et al., 2018). CK's role in plants growth has been discovered, including a role in shoot and root meristem activity, shoots and roots spreading, modulating the size of organs, and developmental progressions like germination and flowering, leaf wilting reduction, etc. (Kieber & Schaller, 2018; Müller, 2011, Werner & Schmülling, 2009). The primary active cytokinins in isoprenoid CKs are DZ. (dihydrozeatin), tZ (trans-zeatin), iP (isopentenyl adenine), and cZ (cis-zeatin) (Kudo *et al.*, 2010; Sakakibara, 2006).

3.1.1 Nutrient stress:

The hormone cytokinin is essential for plants' nutrition absorption. Plants actively take up macronutrients (N, P, K, S) and micronutrients (B, Fe, Si, Se) and carbon, hydrogen, and oxygen.

Among the most crucial nutrients for plant development is nitrogen (N). Thus, a sophisticated network of signaling pathways senses plants internal nitrogen status, as well as N availability and dispersion in their growing media, and generates or regulates integrative reactions to local and protracted signals involving multiple phytohormones (Krapp, 2015; Gent and Forde, 2017; Bellegarde *et al.*, 2017; Guan *et al.*, 2017). The concentration of nitrate controls the transcription of the enzyme (catalase), the first rate-limiting step, isopentenyl transferase (IPT3, IPT5), as well as after the generation of trans-Zeatin (tZ)-type cytokinins, cytochrome P450 (CYP735A2) in Arabidopsis (Kiba et al., 2013; Kieber and Schaller, 2014). Root-derived cytokinins were demonstrated to influence nitrate reactivity and alter essential features such as leaf size (Rahayu et al., 2005) and meristem activity-related variables in the shoot (Muller *et al.*, 2015). Recent studies further suggest that nitrate accessibility changes the shoot apical meristem volume and organogenesis speeds can be explained by the protracted distribution of the CK precursor tZR by altering the expression of WUSCHEL (Landrein *et al.*, 2018).

In plants, potassium (K) is a principal inorganic cation. K deficiency lowers cytokinin levels in Arabidopsis plants, and cytokinin signaling governs root inhibitory action and potassium consumption (Nam *et al.*, 2012). It was also reported that cytokinin-deficient plants were more resistant to potassium shortage. They are linked to increased ROS formation, root hair proliferation, and HAK5 expression, which codes for a potassium uptake transporter.

Boron (B) is necessary for increased plant growth, yet the range between insufficient and hazardous doses is quite limited (Öztürk *et al.*, 2018). According to several studies, ethylene and auxin may control stressful boron responses (González-Fontes *et al.*, 2015). It was established that boron deficit suppresses root meristem growth through a molecular mechanism that involves cyclin CYCD3 suppression mediated by cytokinins (Poza-Viejo *et al.*, 2018). Furthermore, boron increases cytokinin production and the transition of poorly active CKs to highly active versions in oilseed rape (Eggert & von Wirén, 2017). Silicon's positive benefits are mainly mediated via cytokinin (Hosseini *et al.*, 2017). In sorghum and Arabidopsis, silicic acid promotes the CK production gene IPT7, and Si buildup delays dark-induced leaf senescence by activating cytokinin channels (Markovich et al., 2017).

3.1.2 Heat Stress:

High temperature disrupts cellular activities by generating reactive oxygen species (ROS) and denaturing proteins, harming photosynthetic capacity and culminating in a metabolic imbalance. Temperatures regulate CK responses, and CK content may be implicated in a plant's adaptation processes to high temperatures, according to numerous research (O'Brien and Benková, 2013; Pavlu *et al.*, 2018). Endogenous cytokinin levels in Arabidopsis rise due to exposure to heat, especially in the leaves (Dobra *et al.*, 2015), resulting in higher CK levels is responsible for high thermal resistance (Skalak *et al.*, 2016). Extreme heat exceeds the formation of reactive oxygen species (ROS), and increased cytokinin levels can help the antioxidant system eliminate ROS (Xu & Huang, 2006).

Isopentenyl transferase (IPT) inclusion in Arabidopsis seedlings increases endogenous cytokinin levels as well as consequently increases resistance to heat (Skalak *et al.*, 2016). Furthermore, raising endogenous CK concentration using IPT transcription and inhibiting endogenous cytokinin breakdown can help maintain a high cytokinin level.

In rice, high temperature decreases panicle CK quantity and the number of spikelets per panicle. The spikelet number and the proportion of CK are related to the CK redistribution rate through the xylem. The negative effects of heat stress on panicle differentiation and spikelet production are reduced by using CK (Wu *et al.*, 2017). In Arabidopsis, dosing a CK oxidase/dehydrogenase inhibitor improved heat stress adaptability (Prerostova *et al.*, 2020). CK is required for chloroplast function and photosynthetic ability recovery after long-term temperature exposure and alterations in plant developmental programs (Escandón *et al.*, 2016).

3.1.3 Cold Stress:

Cold stress decreases membrane stability, accelerates ion outflow, and nutritional imbalance, among other things. Low-temperature stress also causes the deposition of ROS due to reduced enzymatic activities causing the ROS scavenging system to be dysfunctional. As a result, the large concentrations of ROS have a damaging effect on the membrane, leading

to ion outflow and cellular metabolism disruption (Sui, 2015). The CBF/DREB signaling cascade, also known as the CBF regulon and containing the CBF1 through CBF3 genes as a critical regulatory component, is the most characterized response to cold stress in *Arabidopsis* (Pareek *et al.*, 2017). In *Arabidopsis*, the cold stressor has been linked to CRF genes. The CRF2 and CRF3 genes promoted lateral root stimulation and elongation in response to cold stress (Jeon *et al.*, 2016).

Frost resistance is more vital in *Zoysia* grass at high latitudes (shallow zone). It could be because of the increased carbohydrate content employed as an energy resource and the involvement of phytohormones in controlling plant adaptation to low temperatures (Li *et al.*, 2018). It has been proposed that specific A-type ARR genes are tolerant to cold stress, so the exogenous cytokinin therapy improves wild-type plants' cold tolerance. The stabilizing ARR protein promotes the expression of type-A ARRs in transgenic plants (Shi *et al.*, 2012).

3.1.4 Salt Stress:

Salinity stress deteriorates the several biochemical and physiological mechanisms in plants. Due to variances in CK concentration in saline circumstances, there seems to be no one approach for improving plant salt stress by modifying intrinsic and extrinsic CKs. According to specific research, the CK concentration of rootstock of apple 'robusta' stays high in salinity conditions (Feng *et al.*, 2019), and the cytokinin level in tomato seedlings doubles (Keshishian *et al.*, 2018).

Excess supply of CK in *Arabidopsis* due to IPT8 gene transcription resulted in impaired salinity stress tolerance, linked to increased ROS production and lower activity of ROS-scavenging enzymes (Wang *et al.*, 2015). Applying methyl jasmonate (MeJA) exogenously to wheat might retain significant CK levels by lowering CKX transcriptional activity produced by salt stress, reducing salt-induced seedling development retardation, and boosting salt stress tolerance (Avalbaev *et al.*, 2016).

On the other hand, high cytokinin levels have been demonstrated in experiments to lower the salt tolerance of plants. Upregulation of AtIPT8 in *Arabidopsis* with high cytokinin level decreases crop survival during salt stress by repressing stress-responsive genes, blocking the antioxidant status, and lowering chlorophyll concentration (Wang *et al.*, 2015). Indicated that exogenous cytokinins may be used to boost plant salt tolerance.

3.1.5 Drought Stress:

Drought is the most common abiotic stress having a global impact on agricultural productivity (Daryanto *et al.*, 2016). According to an analysis of wild *Arabidopsis* variations, even subtle dryness can harm plants if they are not genetically acclimated to it (Clauw *et al.*, 2015). Genetically modified barley with increased CK decomposition in its roots had a weaker stress response to long-term drought. It had better stomatal conductance and CO₂ absorption, lower activation of critical ABA metabolism genes, and lowered ABA buildup (Ramireddy *et al.*, 2018).

Many researchers suggest that quantitative as well as qualitative characteristics of root tissues, such as vascular tissue differentiation (Jang & Choi, 2018) and lignification (Pospíšilová *et al.*, 2016), could be essential variables in cytokinin-regulated responses to water-limiting situations. Several researchers have found that the abundance of endogenous plant cytokinins is reduced during drought stress (Calvo-Polanco *et al.*, 2019), so this reduction can improve plant drought tolerance through a variety of physiological responses such as stomatal closure (Naidoo & Naidoo, 2018), early leaf senescence advancement, and leaf dieback (Rivero *et al.*, 2009; Xu *et al.*, 2016; Shen *et al.*, 2014).

3.2 Brassinosteroids (BR.) Against Abiotic Factors:

BR is a distinct category of phytohormones influencing plant growth and development (Nolan *et al.*, 2020). They were initially discovered and identified in the pollen of the *Brassica napus*. The three highly effective BRs, 28-homobrassinolide, 24-epibrassinolide, and brassinolide, are commonly employed in experimental and physiological studies (Vardhini *et al.*, 2006). Recent discoveries reveal that BRs and related chemicals play a stress-impact reducing role in plants exposed to various abiotic stresses.

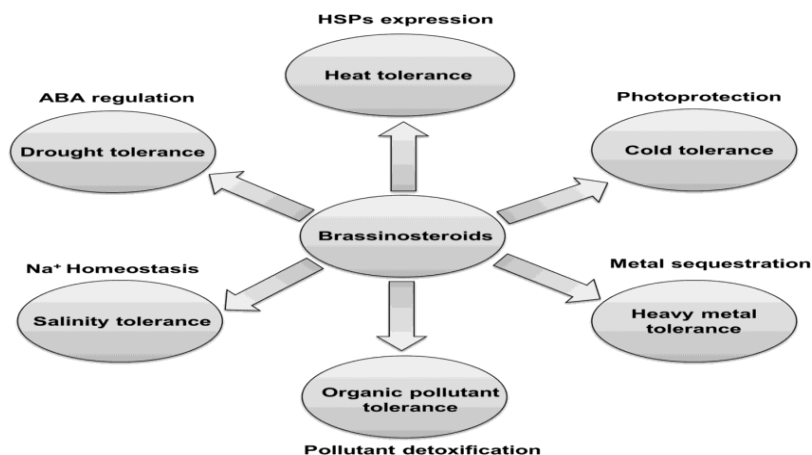


Figure 3: Exogenous brassinosteroid treatment has been shown to enhance plant tolerance to various abiotic stressors.

3.2.1 Drought Stress:

Drought stress is a significant threat to plant growth and metabolism (Niether *et al.*, 2020). It damages the enzyme activities, causes the closing of stomata, lowers seed germination potential, reduces water content, and significantly reduces stem and root length (You *et al.*, 2019). It can be mitigated with the application of BRs (Wang *et al.*, 2019). Under such conditions, Tomato and rapeseed plants have been discovered to have better survival after being processed with EBR. Water stress can also activate related genes, which can be boosted by BR (Li *et al.*, 2021). Under dry conditions, BRs can boost soybean photosynthetic performance, cell water content, SOD activity, proline content, soluble sugar, and lower MDA levels while increasing leaf electrical permeability (Yang *et al.*, 2019).

Drought-induced osmotic stress can hinder normal water uptake by plant cells. Water content and water potential increased after treatment with BRs, enhancing the survival of low-water-potential plants (Wijewardana *et al.*, 2019). Such consequences have also been reported in sugar beet plants that have been subjected to drought. The degree of stress on the beets was linked to a decrease in taproot weight. After treatment with BRs, the reduction in biomass caused by moderate drought conditions was recovered (Chen *et al.*, 2018). Higher biomass in early leaves can contribute to increased acid invertase activity. Increased acid invertase activity could give plants additional assimilative elements. EBR may improve the survival rate of drought-stressed thale cress and rapeseed seedlings and enhance tomato seedlings' relative water content (RWC) (Sahni *et al.*, 2016). EBR treatment enhanced ABA levels and antioxidant enzyme activity while lowering MDA and H₂O₂ levels in the seedling of tomatoes (Ahmad *et al.*, 2018).

3.2.2 Heat Stress:

High temperature emerged as one of the abiotic factors resulting from climate change in the past few years (Nolan *et al.*, 2019). Exogenous BR treatment can help plants cope with the adverse effects of heat (Sadura and Janeczko 2018). Heat stress and exogenous BR cause two distinct types of gene regulation in plants:

- I. BR restores the expression of developmental proteins that have been repressed.
- II. BR causes more significant levels of defensive proteins to be produced.

Under high temperatures, BES1 and BZR1 accumulate at the molecular level, increasing PHYTOCHROME INTERACTING FACTOR4 (PIF4) (Martinez *et al.* 2018). BZR1 effect on gene transcription is aided by the formation of PIF4-BES1 heterodimers, resulting in thermogenic growth. While, a decrease in BRI1 accumulation impacts BR activation, leading to enhanced root development under heat stress (Martins *et al.* 2017).

Exogenous BR treatment stimulates antioxidant enzyme synthesis in a variety of plant species. With the administration of BR, heat-stressed rice plants produced more SOD and POXs [Cao & Zhao, 2006]. While subjected to heat stress, BR treatment in wheat pre- and post-flowering phases enhanced APX and SOD activity [Kumari & Hemantaranjan, 2019].

Plant development and a wide range of physiological responses to high temperatures are said to be regulated by BR. *Ficus concinna* treatment with BR as well as subject to significant heat stress (28, 35, 40 °C) for 48 hours showed a huge rise in reduced glutathione (GSH), oxidized glutathione (GSSG), GSH/GSSG, ascorbate (AsA), oxidized ascorbate (DHA) contents, as well as enhanced enzymatic activities (SOD, POD, CAT, GR, APX) [Jin *et al.*, 2015]. Chen *et al.* (2019) discovered that the administration of 2,4-epibrassinolide may promote the transcription of sucrose transfer genes OsSUT1, OsSUT2, OsSUT4 in young ears under 40 °C, using heat-sensitive rice IR36 as the material and lower the superoxide anion level in the cell membrane, resulting in minor damage.

3.2.3 Cold Stress:

Low temperature affects the plant's shape, physiology, biochemical processes, and cellular structure (Krishna *et al.* 2017; Ma *et al.* 2018), slows plant growth, disrupts photosynthetic processes, and reduces chlorophyll content aborted flower buds, leading to significant productivity as well as economic losses. BR stimulates the genes expression involved in the cellular redox state (GSTX1; likely peroxidase 72, glutathione S-transferase, PER72; CAT2) to decrease the harmful effects of cold stress) (Li *et al.*, 2016).

Using BRs to lessen a plant's cold response to stress is a tried and true strategy. BRs were observed to boost Superoxide dismutase dramatically and Peroxidase activities, raise the quantities of soluble sugar and soluble protein, and lower MDA levels when applied to KY131, KJD6 during the rice booting phase. The grain yield was retained by raising the 1000-grain weight per panicle (Wang *et al.* 2020b). When pepper seedlings were treated with BR, they became more resistant to chilling stress, as evidenced by transcriptome analysis, which showed that under cold stress, BR enhanced the activation of multiple genes in pepper (Li *et al.*, 2016). By stimulating cold stress response genes in *Brassica* and *Arabidopsis*, signal transduction pathways (BR and ethylene signaling network), transcriptional levels of stress response genes (SOD, POD, CAT, GR), and defense systems, BR protects plants from cold stress (Li *et al.*, 2016; Shu *et al.*, 2016).

3.2.4 Salt Stress:

Salinity causes osmotic stress, which negatively impacts growth, development, and agricultural yield. Exogenous BR enhanced chlorophyll content, photosynthetic indices, and antioxidant enzyme activity while lowering ROS and MDA levels, reducing the negative impacts of salinity (Wu *et al.*, 2017). Exogenous BRs could be used in various methods, including seed treatment, root treatment, and foliar application. SIBRI1-, SIBAK1-, and SIDWARF-silenced tomato plants were subjected to salt conditions to evaluate the roles of BR in stress tolerance. The plants were exposed to NaCl (200 mM) for 3 weeks, and it was discovered that plants exposed to saline stress and pretreatment with BRs had a superior growth profile than plants exposed to water solely (Zhu *et al.* 2016).

The BR's isomers play a function in inducing the abiotic stress resistance in plants. Kolomeichuk *et al.* [2020] found that treatment with 24-EBL elevated peroxidase activity and improved the K^+/Na^+ ratio in leaves, which have been likely to account for 24-EBL's salt-stress protection in potato plants. Exogenous EBR administration in black locusts decreases leaf Na^+ content and membrane leakage while increasing the net rate of photosynthesis, stomatal conductance, transpiration rate, chlorophyll level, and PSII maximal quantum efficiency under salinity stress (Yue *et al.* 2018). Even at 30 and 45 days after sowing, foliar treatment of HBL to rapeseed may significantly mitigate the adverse effects of salinity stress (Hayat *et al.* 2012b). Thus, BR contributes to increased tolerance to saline conditions.

CONCLUSION:

Abiotic stresses cause significant growth and development disruptions, decreasing crop yields. Plant responses to abiotic stresses are diverse. The molecular processes governing hormone synthesis, signaling, and action have been elucidated, followed by the involvement of plant hormones in environmental reactions. The promoters stimulate gene transcription during particular growth phases in specific tissue/organs. This difficulty is avoided by transgenic crops responding to specific environmental factors, allowing them to develop under abiotic stress with minimum operational losses. These findings will make it easier to modify hormone biosynthesis pathways to create transgenic plants more resistant to abiotic stress.

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Conflict of interest. The authors declare no conflict of interest among them.

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