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REVIEW
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Potential Role of Plant Growth Regulators in Administering Crucial Processes Against Abiotic Stresses

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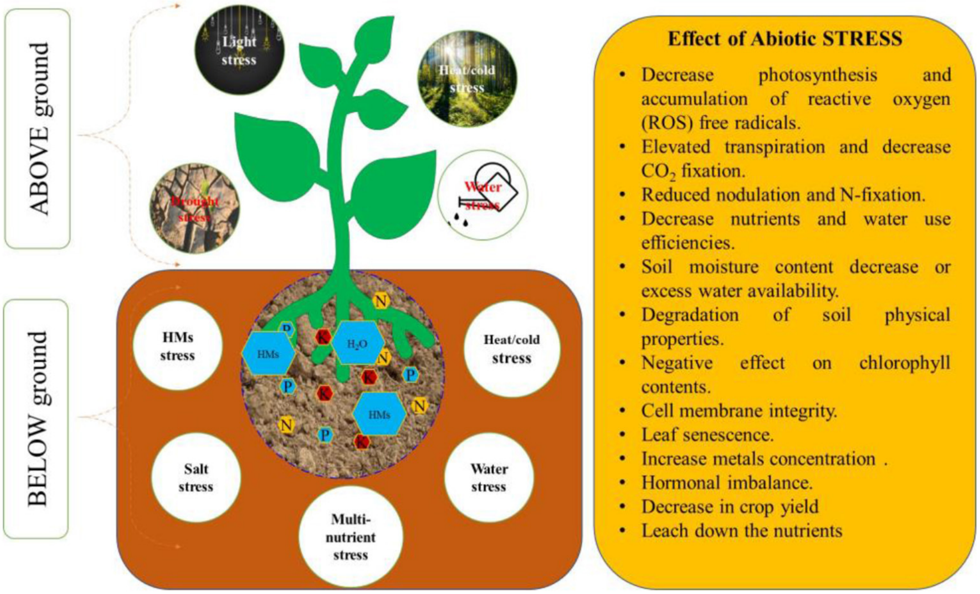
Plant growth regulators are naturally biosynthesized chemicals in plants that influence physiological processes. Their synthetic analogous trigger numerous biochemical and physiological processes involved in the growth and development of plants. Nowadays, due to changing climatic scenario, numerous biotic and abiotic stresses hamper seed germination, seedling growth, and plant development leading to a decline in biological and economic yields. However, plant growth regulators (PGRs) can potentially play a fundamental role in regulating plant responses to various abiotic stresses and hence, contribute to plant adaptation under adverse environments. The major effects of abiotic stresses are growth and yield disturbance, and both these effects are directly overseen by the PGRs. Different types of PGRs such as abscisic acid (ABA), salicylic acid (SA), ethylene (ET), and jasmonates (JAs) are connected to boosting the response of plants to multiple stresses. In contrast, PGRs including cytokinins (CKs), gibberellins (GAs), auxin, and relatively novel PGRs such as strigolactones (SLs), and brassinosteroids (BRs) are involved in plant growth and development under normal and stressful environmental conditions. Besides, polyamines and nitric oxide (NO), although not considered as phytohormones, have been included in the current review due to their involvement in the regulation of several plant processes and stress responses. These PGRs are crucial for regulating stress adaptation through the modulates physiological, biochemical, and molecular processes and activation of the defense system, upregulating of transcript levels, transcription factors, metabolism genes, and stress proteins at cellular levels. The current review presents an acumen of the recent progress made on different PGRs to improve plant tolerance to abiotic stress such as heat, drought, salinity, and flood. Moreover, it highlights the research gaps on underlying mechanisms of PGRs biosynthesis under stressed conditions and their potential roles in imparting tolerance against adverse effects of suboptimal growth conditions.

Keywords: abiotic stress, climate change, crosstalk, nitric oxide, polyamines, stress tolerance

INTRODUCTION

Abiotic stresses (heat, drought, salinity, waterlogging, heavy metals toxicity, soil erosion, etc.) adversely affect the growth, development, and yield of plants resulting in higher economic losses at the expense of global food security (Siddiqui et al., 2019; EL Sabagh et al., 2020b; Hossain et al., 2020). The combined effects of different abiotic stresses on the biological and economic yield of numerous crops are greater than individual stress (EL Sabagh et al., 2019b; Hoque et al., 2020a; Raza et al., 2020; Javeed et al., 2021). Plant growth regulators (PGRs) are naturally biosynthesized by plants which modify growth (increase in branching and rebranching, shoot and root growth, alter or trigger fruit maturing, reproduction etc.) of crop plants and play a significant role in mitigating abiotic stresses (Verma et al., 2016; Takahashi et al., 2019). PGRs also have an important role during stress conditions such as being thermoprotectants, reactive oxygen scavengers, improving photosynthesis, accumulation of stress proteins, and many other regulatory functions related to metabolisms (Akram et al., 2017; Ma et al., 2017; Sharma et al., 2020). The PGRs interrelate with complex signaling systems to equilibrate the responses to evolve eco-friendly strains and thereby, overcome damages caused by stress environmental conditions (Davies, 2013; Suzuki, 2016; Ku et al., 2018; Iqbal et al., 2019). Plants have developed complex mechanisms to detect external signals and can trigger an optimal response against stress conditions under the support of PGRs that mainly control the defensive responses of plants by synergistic and antagonistic activities (called signaling crosstalk) (Adesemoye et al., 2008; Tuteja and Sopory, 2008; Berens et al., 2019; Raza et al., 2019a; EL Sabagh et al., 2021a,b). In this context, PGRs crosstalk with the various inorganic and organic compounds under stress conditions such as nitrates, H_2O_2, H_2S, reactive oxygen species, and NO to balance plant growth and development under unfavorable situations (Kolbert et al., 2019; Vega et al., 2019; Nazir et al., 2020; Xuan et al., 2020). During the stress perception process, there are variations in perceiving various hormonal signals from the early phase to the ongoing phase of stresses, allowing plants to advance to a well-organized growth. There are various ligands and receptors, which help in the perception of hormones. For instance, salicylic acid perceived by NPR proteins, strigolactone perceived and activated by DWARF 14 hydrolase receptor, ubiquitin ligase, leucine-rich receptor repeat kinase, and many other help in the recognition, perception, and signaling of PGRs (LRR-RK) (Chakraborty et al., 2019; Seto et al., 2019; Tal et al., 2020; Wang W. et al., 2020). To consider the above facts, in this review study, the authors discuss PGR-induced physiological adaptations in response to stressful environments, including the interactive effects and cross-talks of different PGRs on plant physiological and biochemical mechanisms under combined abiotic stresses and the potential of exogenous applications as remedies to overcome environmental stresses (**Figure 1**).

Under changing climatic conditions, numerous biotic and abiotic stresses hamper seed germination, seedling growth, and plant development leading to a severe decline in the biological and economical yield of crops (Iqbal and Iqbal, 2015; Abadi and Sepehri, 2016; EL Sabagh et al., 2021a,b; Hong et al., 2021; Shabbir et al., 2021). The biosynthesis of PGRs including gibberellins (GAs), auxin, cytokinin (CT) abscisic acid (ABA), ethylene (ET), jasmonic acid (JA), brassinosteroid (BR), nitric oxide (NO), salicylic acid (SA), and strigolactone (SL) constitutes a potent strategy for plants to respond to stress conditions (Kreps et al.,



Effect of Abiotic STRESS

- Decrease photosynthesis and accumulation of reactive oxygen (ROS) free radicals.
- Elevated transpiration and decrease CO_2 fixation.
- Reduced nodulation and N-fixation.
- Decrease nutrients and water use efficiencies.
- Soil moisture content decrease or excess water availability.
- Degradation of soil physical properties.
- Negative effect on chlorophyll contents.
- Cell membrane integrity.
- Leaf senescence.
- Increase metals concentration .
- Hormonal imbalance.
- Decrease in crop yield
- Leach down the nutrients

FIGURE 1 | Abiotics tree conditions and their effect on the growth and development of plants.

2002; Seki et al., 2002; Raza et al., 2019b; Ahmad et al., 2021). Typically, hormones are interdependent in action by synergistic or antagonistic cross-talk, thereby modulating each of their biosynthesis or responses in a complex way (Aerts et al., 2021). The current review aims to synthesize recent advancements about the roles of PGRs in boosting the defense systems of plants against abiotic stresses (Basu et al., 2021). Also, gaps in knowledge of studied PGR topics have been identified to propose future research perspectives. Furthermore, some perspective compounds especially polyamines have also been objectively discussed due to their similarity of actions with PGRs against different stresses (Chen D. et al., 2019). The article also provides an overview of the recent advances in PGRs in boosting plants' tolerance to various abiotic stresses (**Figure 2**).

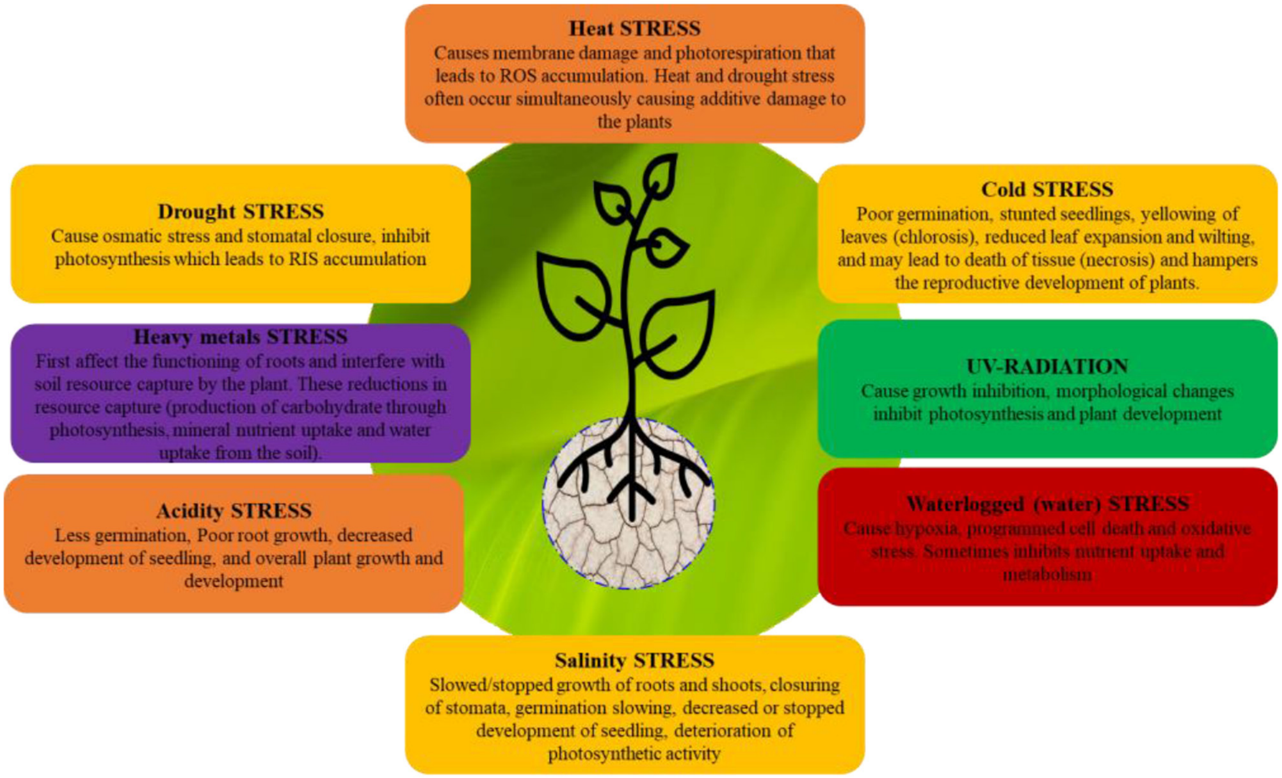
PHYTOHORMONES MEDIATED ABIOTIC STRESS TOLERANCE IN PLANTS

Auxin Induced Physiological and Biochemical Mechanisms for Stress Tolerance

Auxins are vital due to having multiple roles in plant growth and development by influencing various physiological processes including cell elongation, involved in phototropisms and gravitropism, phyllotactic patterning, apical dominance maintenance, and control of root development (Benkova et al., 2003; Blancaflor and Masson, 2003; Blilou et al., 2005; Teale et al., 2006; Holland et al., 2009; Enders and Strader, 2015; Casanova-Sáez and Voß, 2019). Auxins can interact with other hormones on various parameters of the growth and development of cells (Mao et al., 2020; Xu et al., 2020). One example of it is the regulation and transcription of several genes. Many studies have been reported on the association of metabolism, transport, and signaling of auxins in the growth responses of plants under stressful conditions (Shen et al., 2010; Zhang et al., 2012; Kazan, 2013; Remy et al., 2013; Cao et al., 2019; Casanova-Sáez et al., 2021). Thus, more knowledge about the auxin-mediated signaling in the plant stress adaptation responses will help to design strategies for enlightening stress resistance in several crop plants. Furthermore, auxin interacts with stress-responsive signaling components, like calcium (Ca^{2+}) and reactive oxygen species (ROS), which are accumulated in plants during exposure to biotic and abiotic stress conditions (Tognetti et al., 2017). Different stressed conditions could affect the development of stress-induced morphogenic response (SIMR) during different stress tolerance mechanisms of plants (Potters et al., 2007). Auxin biosynthesis in different concentrations under varying abiotic stresses need further investigations in order to explore different factors which tend to trigger auxin production (**Figure 3**).

Auxin Mediated Physiological Changes Under Nutrient Deficiency

Auxin signaling and transport are involved in the stimulation of growth and developmental responses of roots to improve accessibility to nutrients in the soil solution. Primary nutrients like nitrogen, phosphorus, and potassium supplement the crucial role of auxins in boosting the development of lateral roots. Nitrate accumulation and sensing procedures are reported to be associated with alterations in the auxin transport causing rapid changes in the architecture of roots (Krouk et al., 2010; Gojon et al., 2011; Bouguyon et al., 2012; Zhang et al., 2020). Nitrate Transporter1-1 (NRT1-1) protein has a high-activity nitrate influx carrier, which allows the absorption of nitrogen in the form of nitrate (NO_3^-) from the soil along with acting as a nitrate



Heat STRESS
Causes membrane damage and photorespiration that leads to ROS accumulation. Heat and drought stress often occur simultaneously causing additive damage to the plants

Drought STRESS
Cause osmatic stress and stomatal closure, inhibit photosynthesis which leads to RIS accumulation

Heavy metals STRESS
First affect the functioning of roots and interfere with soil resource capture by the plant. These reductions in resource capture (production of carbohydrate through photosynthesis, mineral nutrient uptake and water uptake from the soil).

Acidity STRESS
Less germination, Poor root growth, decreased development of seedling, and overall plant growth and development

Cold STRESS
Poor germination, stunted seedlings, yellowing of leaves (chlorosis), reduced leaf expansion and wilting, and may lead to death of tissue (necrosis) and hampers the reproductive development of plants.

UV-RADIATION
Cause growth inhibition, morphological changes inhibit photosynthesis and plant development

Waterlogged (water) STRESS
Cause hypoxia, programmed cell death and oxidative stress. Sometimes inhibits nutrient uptake and metabolism

Salinity STRESS
Slowed/stopped growth of roots and shoots, closuring of stomata, germination slowing, decreased or stopped development of seedling, deterioration of photosynthetic activity

FIGURE 2 | Overview of abiotic stress and effects on plant growth and development.

feeler and integrate N signal toward root growth (Lay-Pruitt and Takahashi, 2020). NRT1-1 is associated with alterations in lateral root development because NRT1-1 induces the basipetal auxin transport, thereby, inhibiting the auxin accumulation in lateral root and their growth under low NO_3^- concentrations in the soil solutions. On the other hand, at elevated NO_3^- stages, NRT1-1 regulates the transport of auxins inducing their accumulation in lateral root and promoting the growth of this organ (Krouk et al., 2010; Gojon et al., 2011; Bouguyon et al., 2012, 2016).

Similarly, *TINY ROOT HAIR 1* (*TRH1*) gene isolated in roots of *Arabidopsis* plants encoding a KT/KUP/HAK family protein was associated with controlling potassium (K^+) and auxin passage (Vicente-Agullo et al., 2004; Sustr et al., 2019). Impairment of *trh1* in *Arabidopsis* plants caused harmful effects on root hair development, alterations in the gravitropism responses, and a lower capacity to convey K^+ (Rigas et al., 2001; Sun et al., 2020). Auxin-linked low phosphate mediated lateral root development was controlled by auxin receptor genes/proteins such as SIZ1, AFB2, AFB3, and AXR3/IAA7 (Pérez-Torres et al., 2008; Kazan, 2013). Further in-depth studies need to be conducted to explore the gene receptors which modulate its synthesis under specific nutrients deficiency.

Other metal ions like sulfur (S), copper (Cu^{2+}), cadmium (Cd), aluminum (Al^{3+}), boron (B), and iron (Fe) tend to alter the expansion and growth of lateral roots by modifying the root architecture of plants by hampering auxin biosynthesis, signaling, and/or passage pathways (Dan et al., 2007; Lequeux et al., 2010; Mattiello et al., 2010; Martín-Rejano et al., 2011; Peto et al., 2011; Aquea et al., 2012; Giehl et al., 2012; Hu et al., 2013; Yuan et al., 2013). Thus, it has been widely inferred that auxins tend to modify and alter root architecture especially when plants are exposed to nutrient deficiency.

Auxin Mediated Physiological Changes Under Drought Stress

Modifications in root architecture are vital in coping with water scarcity and soil salinity. Auxins regulate hydrotropism responses through which plants roots sense and subsequently, respond to soil moisture (Kaneyasu et al., 2007). The transition from cell division to cell differentiation in roots of *Arabidopsis thaliana* plants was auxin minima dependent (Di Mambro et al., 2017). Auxins, in conjunction with ABA, promote root hair growth due to the two antagonistic phenomena called gravitropism and hydrotropism which occur concurrently in the soil. The contribution of auxin in hydrotropism is less than gravitropism (Cassab et al., 2013). However, the ultimate direction of root extension in the direction of moist areas of the soil is primarily controlled by ABA signaling, which can be overwhelmed by the auxins mediated gravitropism (Taniguchi et al., 2010). Xu Q. T. et al. (2013) inferred that the ABA regulates primary root and root hair growth by mediating the auxin passage in both *Arabidopsis thaliana* and *Oryza sativa* plants. Furthermore,

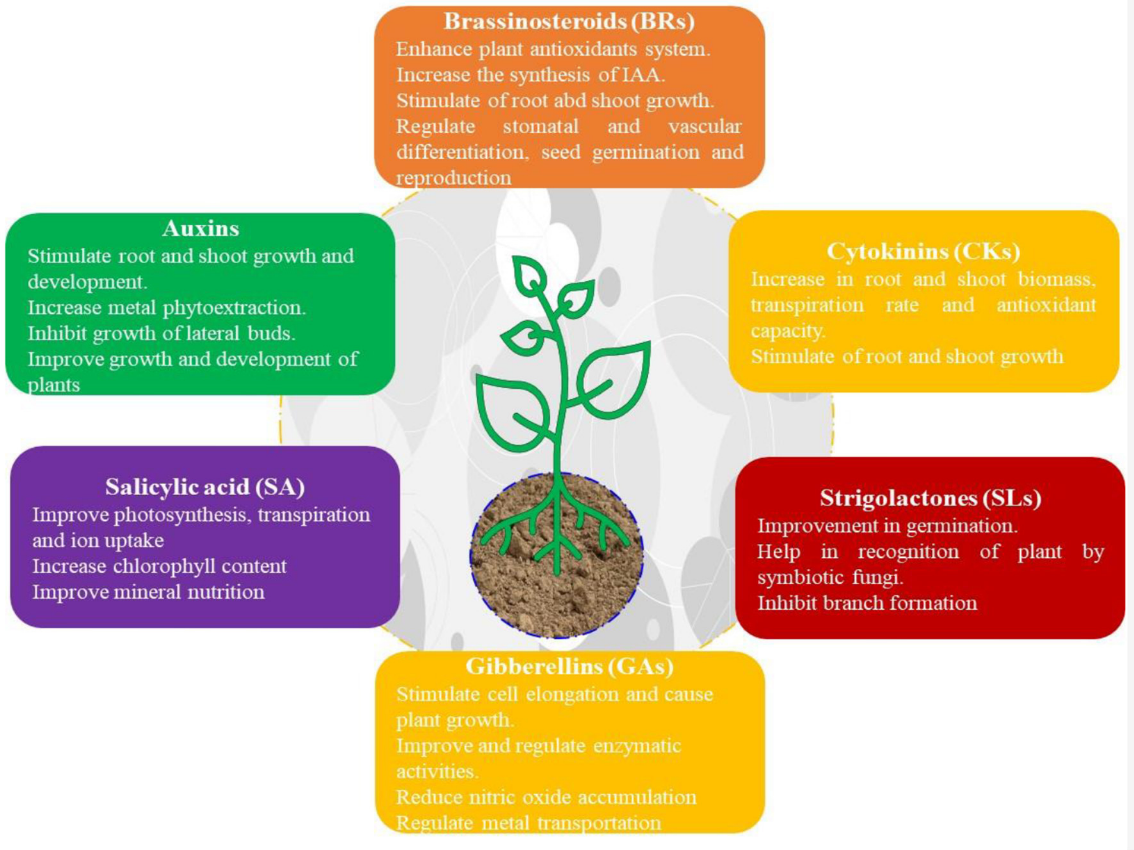


FIGURE 3 | Role of selected PGRs on plant growth and development.

it causes an increase in the proton secretion process by the accomplishment of plasma membrane-bounded H-ATPases and maintains root elongation.

More studies are required to separate the complex connections among auxin and other PGRs on modifications in root architecture, which can be modified in plants under stress conditions (Indu Lal et al., 2021). A hydrolase called IAA-Ala Resistant-3 (IAR3) in *Arabidopsis* plants modulated root architecture throughout osmotic conditions (Kinoshita et al., 2012) and has a capability of producing free auxin by hydrolyzing auxin indole acetic acid (IAA) forms in roots under drought (Rampey et al., 2004). Thus, IAR3 is proposed to be a bioactivator of auxin generation and thereby stimulating lateral root development under water deficit soils to survive in such extreme environments (Kinoshita et al., 2012).

Genome-wide expression analyses of plants confronting water deficit conditions often indicate distinguishingly expressed auxin-connected genes. For example, MIZU-KUSSEI (MIZ1) protein in *Arabidopsis* regulates auxin levels and increases primary and lateral root growth under water stress conditions (Miyazawa et al., 2012). The auxin-responsive genes encoding several associates of the ARF transcription factor (TF) family were also differentially expressed in *Glycine max* roots of plants under water deficit environments. These genes could act as potential candidates for the breeding of water deficit tolerant soybean cultivars (Ha et al., 2013).

In a study, *Arabidopsis* activation-tagged *yuc7-1D* mutant showed enhanced expression of the stress-correlated genes *RD29A* and *COR15A*, which augmented the drought resistance of plants (Lee et al., 2012). Similarly, the *Arabidopsis YUCCA* gene in the drought tolerance responses regulate the auxin invention when it was articulated in potato plants (Kim et al., 2013). The increased expression of YUCCA protein, CONSTITUTIVELY WILTED1 (Woo et al., 2007), and supposed auxin efflux transporter OsPIN3t are complicated in the maintenance of water homeostasis in rice plants (Zhang et al., 2012). Recently, the *Arabidopsis* SMALL AUXIN UP RNA 32 (SAURs) protein regulates the drought adaptation through modulating ABA transduction (He et al., 2021). Likewise, *INDITTO2* transposons convey auxin mediated *DEEPER ROOTING 1* (DRO1) transcription factor for drought avoidance in rice (Zhao et al., 2021). However, auxin synthesis with respect to crop growth stage under varying extent and duration of drought stress must be studied to increase our understanding regarding the ameliorative effect of auxin in drought-stressed plants.

Auxin Mediated Physiological Changes Under Salt Stress

Salinity drastically affects plants by exerting physiological drought resulting from high osmosis in soil solution and causing ion imbalance due to high solubility of certain minerals hampering root development (Islam et al., 2011; EL Sabagh et al., 2019a, 2020a; Liu et al., 2020). Mild saline conditions caused a decrease in the elongation of lateral roots and increased lateral root sizes, while high salt conditions inhibited the root development (Zolla et al., 2010). The salt stress could be regulated by the synergism of many signaling molecules such as phytohormones with auxin as a key mediator (Ribba et al., 2020). The salt responsive auxin signaling genes, *AXR1*, *AXR4*, *IAR4,* and *TIR1* enhanced lateral root development in plants under salt environments. In contrast, the lateral root development was reduced in the mutants *axr1*, *axr4*, and *tir1*, iar4 and it was impaired in the auxin invasion mutant *aux1* (Wang Y. et al., 2009; Zolla et al., 2010; Fu et al., 2019). The circulation of auxin efflux transporters (PIN2) regulates the gravitropism responses through the changes in basipetal auxin transport, which could be involved in growth responses associated with decreasing the consequences of salinity in plants (Vanneste and Friml, 2009; Galvan-Ampudia and Testerink, 2011). The salt overly sensitive (SOS) genes, such as *SOS1-3,* are obligatory for salt resistance responses in *A. thaliana* (Ji et al., 2013). These genes are associated with the auxin-mediated lateral root formation in plants under salinity (Yang et al., 2008). Plant roots grown in highly acidic soils exhibit vast transcriptional modifications in the expression of some auxin-related genes, implying auxin-mediated alterations on root architecture (Lager et al., 2010). The PIN2 maintained buffering of extreme soils was observed in roots of plants growing in alkaline conditions where auxin transport activity is mediated by PIN2 followed by auxin-mediated activation of plasma membrane H^+-ATPase and photon emission in the root tips (Xu Q. T. et al., 2013). Auxin biosynthesis and transportation in response to specific salt stress should be further studied to understand the underlying mechanism of auxin modulation.

Auxin Mediated Physiological Changes Under Flooding or Waterlogging

Different abiotic stresses such as flooding, submergence, or waterlogging cause either hypoxia or anoxia depending on plant species. These responses include an increase in aerenchyma development, adventitious root development, and shoot development along with epinastic or hyponastic growth phenomena, among others (Jackson, 2002; Visser and Voesenek, 2004; Voesenek et al., 2006; Bailey-Serres and Voesenek, 2010; Lin et al., 2017). Ethylene trap by water would break new ground alarming signals to the plant, indicating waterlogging. Flooding or waterlogging-dependent adventitious root production requires both increased auxin accumulation and altered auxin transport, together with an enhanced ethylene invention (Vidoz et al., 2010). Further, it was found that ethylene induces the auxin transport through auxin flux to the flooded portions of the tomato plants resulting in a novel root organization, which can substitute the root system injured during their submergence. The auxin transport is necessary for adventitious root development in tobacco and rice plants (McDonald and Visser, 2003; Xu et al., 2005; Yamauchi et al., 2019). Overall, there is complex cross-talk between stress hormones ET and auxin the modulation of growth or development of lateral and adventitious roots under waterlogged plants (Muday et al., 2012; Hu et al., 2018).

Auxin Mediated Physiological Changes Under Oxidative Stress

The oxidative stress under abiotic stress alters redox status in cells which gives rise to the biosynthesis of ROS (Fahad et al., 2019). The controlling mechanisms of ROS biosynthesis redox homeostasis involve key regulators like thioredoxin (TRX) and glutathione (GSH) (Hasanuzzaman et al., 2020). These regulators participate in the growth and developmental processes through the modulation of auxin signaling (Bashandy et al., 2010). Thus, lack of thioredoxin and glutaredoxin in triple mutants of *Arabidopsis* (two genes encoding *NTRA* and *NTRB*) cad2 showed perturbed auxin passage (Bashandy et al., 2010). Terrile et al. (2012) demonstrated that nitric oxide (NO) also played a part in the optimum process of auxin signaling by inducing the breakdown of AUX/IAAs during lateral root formation. Root growth of rice in Cd-stressed soils has been reported to be regulated by the interaction of H_2O_2 and auxin signaling where enhanced H_2O_2 regulates the gene expression of auxin signaling, showing strong links between auxin signaling pathways and ROS synthesis under stressful conditions (Zhao et al., 2012; Zwiewka et al., 2019).

The rapid auxin-reliant hindrance of root formation and early stage of root gravitropism responses are regulated by the TIR1/AFBauxin co-receptors. One of which, called AFB1, has an essential role in these responses (Prigge et al., 2020). The loss of function mutations of TIR1/AFB2 seedlings showed reduced salt sensitivity. In contrast, in seedlings experiencing oxidative stress, double receptor mutants of tir1 afb2 and tir1 afb3 showed an augmented percentage of primary root formation and cell death induced by H_2O_2. Together, the antioxidant defense enzymes like catalase (CAT), ascorbate peroxidase (APX), and ROS-degrading enzymes such as glutathione *S*-transferase 1 (GST1), cytosolicAPX1, and a zinc finger TF (*ZAT12*) were in *tir1 abf2* plants under saline conditions. These results suggest that the decrease of auxin signaling pathways may be utilized by plants to improve tolerance against oxidative stress (Iglesias et al., 2010; Pasternak et al., 2020).

Auxin signaling interacts with shade avoidance mechanisms and communicates with different plants in the rhizosphere (Faget et al., 2013; Falik et al., 2013) as a sensor for detecting other roots in close plants (Fang et al., 2013), regulating the communication between the roots of the plant itself, or with neighboring plants and also in the root-shoot communication (Kabouw et al., 2012). The complex connections among auxin and other PGRs play essential roles in stress-associated developmental modifications in auxin biosynthesis, signaling, or carriage mutant plants (Bielach et al., 2012; Muday et al., 2012; Rahman, 2013; Shani et al., 2013; Sereflioglu et al., 2017). However, a comprehensive understanding of these interactions has not yet been reported.

Gibberellin Induced Physiological and Biochemical Mechanisms of Stress Tolerance

Gibberellins play key roles in plant growth and development (**Figure 3**) along with their physiological (cell division, seed dormancy, germinations, etc.) and biochemical processes (Olszewski et al., 2002; Hedden and Thomas, 2012; Tanimoto, 2012; Vishal and Kumar, 2018; Islam et al., 2021). The inhibition of the biosynthesis of GAs is the primary mode of action (Rademacher, 2000), followed by retarded growth and dwarf growth habit in plants under stress environments. Suppression of GA signaling through alternative splicing is the common response to abiotic stresses, which is accompanied with up-regulation and fine tuning of GA2ox, CsGA2ox8 (encoding GA-inactivating enzymes), and DELLA (negative controller of GA signaling) (Achard et al., 2006, 2008a,b; Lo et al., 2008; Rieu et al., 2008; Liu et al., 2021). Likewise, genome wide expression analysis of GA2ox, GA3ox, and GA20ox are related to oxidase gene under multiple stresses. However, the mechanism of GA signaling in stress tolerance is less explored compared to the role of GA as a growth-promoting controller (Colebrook et al., 2014).

The GA2-oxidases (GA2ox), DELLA domain proteins, GAI (GA insensitive), and RGL1 (repressor of ga1-3 like), are vital in GA regulation and signaling in stress environments. GA2oxs inhibit bioactive GAs leading to dwarfism (Lo et al., 2008; Rieu et al., 2008). Activation of DELLA domain proteins is essential for surviving in stress environments (Achard et al., 2006, 2008a,b; Zhou and Underhill, 2017) as it causes inhibition of cell proliferation and expansion (Olszewski et al., 2002; Claeys et al., 2012). The role of GA in various physiological processes governing growth under various abiotic stresses has been documented. However, a detailed underlying mechanism of GA signaling in each response is still needed to be further explored (Colebrook et al., 2014).

Gibberellin Mediated Physiological Changes Under Flooding or Waterlogging

The GA-mediated signaling under submergence could be best explained using rice genotypes modified to tolerate flooding stress (Bailey-Serres and Voesenek, 2010). The most common strategy to escape long-term flooding is rapid inter node elongation, allowing the shoots to out-grow the flood waters. The internode development is mediated by ethylene due to activation of the ERF domain proteins named SNORKEL1 and SNORKEL2 (Hattori et al., 2009), which leads to the accumulation of GA in submerged rice plants. The expression of gene submergence tolerance-1 (Sub1A) (Xu et al., 2006) provides an escape to short-term deep flooding through inhibiting shoot elongation and relates to improved levels of DELLA protein SLR1 and the negative controller of GA signaling SLRL1 in rice (Bailey-Serres and Voesenek, 2010; Claeys et al., 2014). The *Sub1A* gene enhances leaf viability and promotes leaf growth under submergence (Fukao et al., 2006) and similar related escape responses such as hyponasty. Particularly, due to variance growth of the petiole, leaf blade formation was observed in *Rumex palustris* at submergence (Polko et al., 2011). Flooding escape is controlled by two ERFs, namely, SNORKEL1 (SK1) and SNORKEL2 (SK2) which activate internode development through GA during flooding stress (Hattori et al., 2009).

Gibberellin Mediated Physiological Changes Under Osmotic and Salt Stress

Gibberellin mediates osmotic adjustments in response to salt stress (Skirycz et al., 2011; Claeys et al., 2012). GA, together with ET and ABA, regulates cell proliferation and expansion in *Arabidopsis* leaves during abiotic stresses (Skirycz et al., 2010). In addition, ET and GA coordinately regulate the cell cycle and cell proliferation of *A. thaliana* exposed to salt stress (Skirycz et al., 2011; Claeys et al., 2012). The ethylene and GA-arbitrated responses are related to ERF as a dominant activator of both inhibition of leaf growth and initiation of stress tolerance genes (Claeys et al., 2012) where DELLA acts as a conjunction of numerous hormone signaling pathways in stress situations (Achard et al., 2006; Fukao and Bailey-Serres, 2008).

Gibberellin Mediated Physiological Changes Under Drought Stress

Drought stress lowers water availability and nutrients accessibility to the roots which affects crop growth and yield. Drought reduces GA accumulation and impaired membrane stability resulting in cell damage in maize leaves (Wang et al., 2008). Drought stress also reduces GA signaling, leaf area, and transpiration rate, which enhances water use efficiency in plants. The decreased GA2ox expression in the roots (Krugman et al., 2011) and lateral roots elongation is linked with a cross-talk among GA and IAA (Gou et al., 2010; Chen Z. et al., 2019) in the roots in response to drought. Root-derived signals maintain root growth and reallocate photo-assimilates to adjust the growth of shoot and root. ABA-mediated root signals that cause stomatal closure seem to be the result of crosstalk of ethylene and GA (Coelho Filho et al., 2013). However, root-derived signals do not regulate leaf growth and leaf metabolism. As such, regulation is mediated by leaf/shoot GA (Kaneko et al., 2003). In *Arabidopsis*, drought stress increased the expression of *DELLA* and *XERICO* genes, which cause growth inhibition but increase the survival of plants (Achard et al., 2006; Zentella et al., 2007). The impaired GA activity and suppressive signaling facilitate shoot growth under drought stress. Water deficit conditions and short-day photoperiod prompted modulation of a group of GA2ox and DELLA protein-encoding genes which are downstream of diverse signal transduction ways (Zawaski and Busov, 2014).

Cytokine-Induced Physiological and Biochemical Mechanisms of Stress Tolerance

Cytokinins play key roles in regulating plant cell discrepancy, delaying leaf senescence (Sakakibara et al., 2006), and other main developmental progressions such as governing integrate compounds apportioning (Ronzhina and Mokronosov, 1994), sink asset (Kuiper, 1993), and source/sink associations. The *ISOPENTENYL TRANSFERASE* (*IPT*) encoding enzyme catalyzes cytokinin (CK) synthesis, increased the sink capacity, and militarizes nutrients to the cells or tissues where they are utilized. Altered sink/source associations were detected in CK-lacking tobacco shoots and roots (Werner et al., 2008). The stress-induced CK synthesis improved N and C assimilation associated with enhanced sink in the transgenic plants during water stress, which characterized physiological responses and metabolic pathways connected with the CK persuaded stress resistance in P_{SARK}::*IPT* transgenic rice plants (Reguera et al., 2013). The CK-regulated N uptake controls the N levels in the plant (Kiba et al., 2011) where C-N interaction regulates CK biosynthesis in response to soil N availability (Sakakibara et al., 2006). Transgenic P_{SARK}::*IPT* rice plants showed CK mediated higher N assimilation in a C-N-dependent manner (Reguera et al., 2013). It was assumed that a decrease in root tip turgor can disturb the synthesis and passage of CKs in the root tip and simultaneously abridged their passage along with the accumulation of nutrients that are available in the soil under drought stress (Davies et al., 1986; Pavlu et al., 2018).

Cytokinin Mediated Physiological Changes Under Drought Stress

High CK concentrations (**Figure 3**) in plants tend to delay leaf senescence, increase proline levels, and survival of plants under water-stress conditions (Alvarez et al., 2008). The overexpression of the isopentenyl transferase gene (*IPT*) and related promoters such as PSAG12 (Gan and Amasino, 1995) in different plant species showed a substantial delay in plant senescence followed by delayed flowering and reduced yield (Ma, 2008). This is inferred to be due to altered source/sink relationships.

Enhanced CK levels boosted the existence of plants under water deficit environments (Rivero et al., 2007). Use of promoter (*SARK*; a maturation- and stress-induced promoter) upstream to IPT for overexpression in both monocots and dicots induced drought tolerance (Rivero et al., 2007; Peleg et al., 2011; Qin et al., 2011). The transgenic P_{SARK}::*IPT* rice showed altered hormone synthesis and hormone regulatory pathways, thereby modifying source/sink relationships, subsequently higher grain yield is obtained under the water stress environment (Peleg et al., 2011). Water deficit decreased photosynthetic activity and respiration resulting in lower internal CO_2 in plants (Lawlor and Tezara, 2009). However, transgenic P_{SARK}::*IPT* rice (Reguera et al., 2013) and transgenic tobacco plants expressing P_{SARK}::*IPT* (Rivero et al., 2009) increased internal CO_2 level so that photosynthesis continues as that of normal plants because increased biosynthesis of CK safeguards the biochemical procedures related to photosynthesis under water-limited conditions. Reduced CK levels concomitantly induce ABA activity inducing stomatal conductance and hindering photosynthesis under drought stress (Rivero et al., 2010). Stress persuaded CK synthesis regulated by the stress-induced promoter, protecting harmful effects on the photosynthetic device, which allows better photosynthetic tariffs and higher yield under drought stress in tobacco (Rivero et al., 2009), peanut (Qin et al., 2011), and greenhouse-grown cotton (Kuppu et al., 2013).

Cytokinin Mediated Physiological Changes Under Nutrient Deficiency

Nutrients in growing media are detected by a complex system of signaling pathways generated by integrating PGRs (Krapp, 2015; Bellegarde et al., 2017; Gent and Forde, 2017; Guan et al., 2017; Awad et al., 2021). There are many genes such as isopentenyl transferase (IPT3, IPT5), P450 (CYP735A2), auxin response regulators (*ARR*s), cytokinin response factors (*CRF*s), and glutaredoxin genes (GRX) that regulate the CK biosynthesis and nitrate signaling (Pavlu et al., 2018). Long-distance shoot and root-derived CK mediates nitrate responses and control key characters, e.g., leaf size (Walch-Liu et al., 2000; Rahayu et al., 2005) and meristem activity-related traits (meristem size and organogenesis) (Müller et al., 2015). The cell cycling in shoot and root meristems regulates the magnitude of inorganic phosphate (Pi) that, in turn, gets mediated by CK (Schaller et al., 2015). Potassium deficiency decreases CK level which induced root growth affecting potassium uptake (Nam et al., 2012). CK mediated GSH homeostasis and GSH breakdown play a physiologically significant role in nutrient utilization, especially during sulfur (S) deficiency (Bhargava et al., 2013). Boron (B) deficiency impairs root meristem development by impairing molecular machinery connecting the CK-mediated suppression of cyclin CYCD3 (Poza-Viejo et al., 2018).

Cytokinin Mediated Physiological Changes Under Salinity Stress

Increased CK levels enhance photosynthesis under salt stress by stimulating the expression of genes that promote the biosynthesis of chlorophyll (Ma et al., 2016). The overexpressed CK-degradation enzyme (*CKX*) in *Arabidopsis* plants showed enhanced CK biosynthesis followed by high CO_2 assimilation (Cerný et al., 2013) whereas AtCKX1 mutants showed reductions in CO_2 acclimatization rates, accompanied by lower stomata closure (Vojta et al., 2016). Further, CKs improve the potential of antioxidant defense systems that could protect their cells from stress-induced ROS gathering, protecting chloroplast integrity (Rivero et al., 2007; Zavaleta-Mancera et al., 2007), dropping electrolyte leakage and/or increasing malondialdehyde (MDA) levels (Liao et al., 2017; Xu et al., 2017). Cytokinin affects root and shoot development along with other agro-botanical traits under a water-limiting environment (White and Kirkegaard, 2010). Particularly, it decreases root to shoot hypocotyl relations, improves root growth, nutrient uptake, and enhances tolerance to water-limiting conditions (Pospíšilová et al., 2016). Further qualitative traits such as variation of vascular tissue and lignification of root tissues showed CK-regulated reactions to water-limiting environments (Pospíšilová et al., 2016).

Abscisic Acid-Induced Physiological and Biochemical Mechanisms of Stress Tolerance

Abscisic acid is one of the widely examined stress hormones which are well-correlated with the intensity of stress tolerance in crop plants. It coordinates an array of functions in plants, enabling them to withstand a variety of abiotic stresses

(Finkelstein, 2013; Wani and Kumar, 2015; Raza et al., 2019b). It is well-reported that abscisic acid (ABA) accumulation increases in response to abiotic stresses such as drought, salt, and cold (Zhang et al., 2014; Vishwakarma et al., 2017; Malaga et al., 2020). The elevated level of ABA enables plants to cope with salt and drought by improving cellular dehydration and water balance. Besides, ABA regulates key processes like leaf abscission, inhibition of fruit ripening, and seed development (Zhang et al., 2014). Moreover, it also regulates multiple physiological processes by acting as signaling mediators to impart adaptation to abiotic stresses (Sah et al., 2016). ABA-induced gene expression is responsible for the quickest response to abiotic stress in plants (Yamaguchi-Shinozaki and Shinozaki, 2006). The rapid expression of short-term ABA stimulated genes facilitates plants to endure under unfavorable growing environments (Nemhauser et al., 2006).

The ABA-mediated stomatal closure under stress conditions suggests that cross talks with hormones such as JA, SA, BR, CK, NO, and ET also influence stomatal function (Acharya and Assmann, 2009). Exogenous application and/or cold stress-induced ABA synthesis enhances cold tolerance of plants, thus representing the role of ABA in plant adaptations to cold stress (Xue-Xuan et al., 2010). In addition, ABA works as a multipurpose mediator of numerous physiological processes. ABA plays a crucial role in stimulating seed dormancy, hindering seed germination and shoot growth while, on the other hand, promoting root growth, leaf senescence in plants switching from vegetative to reproductive phase to complete life cycle under low water potentials. Furthermore, ABA, in coordination with auxin, can enhance root hair formation in *Arabidopsis* (Shibata and Sugimoto, 2019). The gene expression analysis concluded that ABA could control plant expansion by reducing the signal transduction or biosynthesis of numerous growth-promoting PGRs such as CK, GA, and BRs at the transcriptional or post-translational levels (Zhang et al., 2009a,b; O'Brien and Benkova, 2013; Fahad et al., 2015; Sah et al., 2016).

ABA-Mediated Physiological Changes Under Drought Stress

The moisture stress coupled with other environmental stresses, i.e., extreme temperature and salt, promote the synthesis of ABA in plants (Cutler et al., 2010; Kim et al., 2010). Classical physiological alterations in plants under water deficit stress include less root water absorption, low water potential, and turgor in the leaves, reduced leaf elongation, stomatal closure, modification in gene expression, and ABA-dependent adaptive physiological responses like modulation of root architecture (Clark et al., 2005; Harris, 2015). Plants have evolved an array of adaptive mechanisms to withstand water scarcity such as differential shoot and root growth. Early root growth promotion at the expense of shoot (hypocotyl) growth inhibition is probably mediated by ABA in *Vigna radiata* under mild water stress (Das and Kar, 2018). ABA is also considered as a prime signaling cue l for root-to-shoot stress (Schachtman and Goodger, 2008). It plays a role in drought stress tolerance in two ways: inducing cellular dehydration tolerance and maintaining water balance. Dehydration tolerance proteins within plant cells are encoded by gene expression, while guard cell regulation enables plants to achieve water balance. Excessive ABA is produced in response to osmotic stress resulting inactivation of ABA biosynthesis and inhibition of ABA degradation (Zhu, 2002). The biosynthesis of ABA in roots induced with soil drying and elated *via* the xylem to the shoot (Wang et al., 2000; Dodd, 2005). Different transgenic plants over-expressing ABA-biosynthesis genes had a greater ability to withstand water deficit stress. Genes, namely, *AtNCED3* and *NCED*1 in *Arabidopsis,* play a critical function in ABA biosynthesis under drought. SgNCED1 overexpressed tobacco plants showed increased leaf ABA and tolerance to drought and salinity (Peleg and Blumwald, 2011). Overexpression of *LeNCED1* showed increased ABA accumulation and ERA1 in transgenic canola (*Brassica napus* L.), which exhibited higher yield when grown under mild drought stress. Stomatal closure is a vital water conservation strategy in drought-tolerant plants, which is regulated through ABA-triggered complex series of events (Turner et al., 2001). Applied exogenous ABA and glycine betaine (GB) alone or in combination improved drought tolerance in all accessions of *Axonopus compressus* (Nawaz and Wang, 2020).

As ABA interacts with plant hormones under drought, it results in reducing CK levels, showing antagonistic effects between CK and ABA (Peleg et al., 2011). High ABA and low CK concentration facilitate the stomatal closure and decrease water loss *via* transpiration under water deficit stress (Morgan, 1990). Thus, indicating the role of ABA in inducing drought tolerance in crop plants. On the other hand, ABA and ET work together to hamper seedling growth (Cutler et al., 2010) but control seed growth antagonistically (Ghassemian et al., 2000). It inhibits BR-triggered responses in plants exposed to several abiotic stresses (Divi et al., 2010). The ABA signaling components ABI2 (abscisic acid insensitive 2) and GSK3s co-regulate a network of stress-responsive genes to inhibit BR signaling in plants when exposed to abiotic stress (Wang et al., 2017). Several aspects of plant growth or development are controlled by BR and ABA antagonistically in a range of environmental stresses. The ABA-associated chemical signals that arise due to environmental stresses have a great influence on certain physiological processes such as the rate of grain-filling in wheat (Yang et al., 2006). On the other hand, CK and ABA are responsible for controlling carbon remobilization and plant senescence in wheat subjected to drought stress (Yang et al., 2003). Short-term ABA facilitates stimulus responses, regardless of the association of ABA to metabolic readjustments (Yang et al., 2014).

Among major abiotic stress factors, drought or moisture deficient conditions affect the root system of plants to a greater extent. Therefore, drought-induced ABA accumulation may be attributed to maintaining root development and shoot progress as a substitute for reduced growth (Farooq et al., 2009). Relative growth alters in response to ABA, like inhibition of leaf area development, higher root-shoot dry weight ratio, and production of deeper roots. Consequently, modulations in the root environment exhibit both systemic and local consequences on ABA-mediated responses (Farooq et al., 2009; Puertolas et al., 2015; Vishwakarma et al., 2017; Afzal et al., 2020).

ABA-Mediated Physiological Changes Under Salinity Stress

Abcisic acid plays a critical role in plant adaptation responses to stress (Sharma et al., 2005). Plants experience osmotic stress and water deficit under salinity stress and respond by inducing ABA biosynthesis in roots and shoots (Cramer and Quarrie, 2002; Cabot et al., 2009). Accumulation of Ca^{2+}, K^+, and other compatible solutes such as sugars and proline are responsible for ABA-induced salinity tolerance (Gurmani et al., 2011). The ABA modulated salt responsive genes play a fundamental role in cellular signaling under salinity stress. ABA-induced expressions of HvVHA-A for subunit A (the catalytic subunit) of vacuolar H^+-ATPase, HVP1, and HVP10 for vacuolar H^+ inorganic pyrophosphatase have been observed in *Hordeum vulgare* under saline conditions (Fukuda and Tanaka, 2006). Similarly, ABA-mediated MAPK4-like, TIP 1, and GLP 1 gene expression have been reported under salinity in wheat crops (Keskin et al., 2010). In addition, ABA has been regarded as a key signaling molecule that stimulates the suppression of lateral root growth when plants are exposed to salt stress (Duan et al., 2013). ABA level elevates absolutely in lateral root cells under salinity stress, which provokes a dormant period in post-emergence lateral roots. A well-developed and thick casparian strip is formed in lateral roots during the dormant period acting as a barrier to minimize Na^+ ions diffusion *via* the endodermis. ABA signaling is activated within endodermal cells in the presence of Na^+ ions that seize growth, thereby restricting elongation of lateral roots under elevated salinity conditions (Fernando and Schroeder, 2016). PYL8/RCAR3 ABA receptor has been described to function in ABA-mediated restriction of primary root growth and improvement of lateral root growth when exposed to ABA (Zhao et al., 2014). Furthermore, it shows differential responses toward the plant antioxidant system under abiotic stresses. The up-regulation of antioxidant activity in callus cells of the cotton crop is attributed to the ABA-mediated signal transduction pathway (Bellaire et al., 2000). Higher activity of antioxidant enzymes in bermuda grass (Lu et al., 2009) and wheat (Agarwal et al., 2005) has been linked to ABA synthesis under salinity stress. ABA synthesis and accumulation of ROS occur under salinity stress. Thus, calcium and/or H_2O_2 act as second messengers of ABA-induced stomatal closure and expression of genes in response to several abiotic stresses (Zhu, 2002; Asad et al., 2019). A comparative rise in ABA concentration is generally connected with soil water or leaf potential in plants exposed to salt stress (Zhang et al., 2006). The expression of salt-associated genes is usually controlled by ABA-mediated signaling, which enables plants to survive salinity stress (Keskin et al., 2010). Likewise, plant water status through guard cells and growth is regulated by ABA-induced expression of genes (Zhu, 2002).

Under a saline environment, ABA triggers plant protective mechanisms that regulate the expression of genes persuaded by salt stress (Shakirova et al., 2003; Parida and Das, 2005; Sah et al., 2016). A significant concentration of ABA accumulates in the leaves of salt-tolerant *maize* hybrids under salt stress. As a growth pre-requisite, an increase in ABA is necessary for acidifying the apoplast (Zorb et al., 2014). Mediating leaf expansion and restricting Na and Cl in leaves is a well-reported facilitating role of salt-induced ABA (Cabot et al., 2009). The ABA synthesis improves stomatal conductance which gets disturbed under salt stress. The ABA regulates stomatal closure resulting in reduced water loss through transpiration (Wilkinson and Davies, 2010; Sah et al., 2016). The stomatal closure in plants growing under salinity might be attributed to ABA-induced higher Ca concentration in the cytoplasm. ABA-induced augmentation of H_2O_2 production activates ion channels present in plasma lemma and regulates turgor losses through guard cells (Kim and Wang, 2010). The ABA plays a vital role in the synthesis of osmoprotectants (Sah et al., 2016) like proline (Iqbal et al., 2014; Fahad et al., 2015) and dehydrins in response to ROS production under salt-stress-induced dehydration (Javed et al., 2020). Expression of the *OsP5CS1* gene stimulated by salinity is associated with a rise in endogenous ABA concentration. The exogenous supply of 100 μM ABA in rice seedlings had an ameliorated survival degree by 20% and elicit proline uptake by triggering the expression of *OsP5CS1* gene in rice (Sripinyowanich et al., 2013). Thus, a positive correlation between ABA accumulation and salinity resistance was revealed in terms of synthesis and accumulation of compatible solutes, including proline and sugars, and K^+ and Ca^{2+} in vacuoles of root cells, which counteract with Na^+ and Cl^- uptake (Gurmani et al., 2011). Moreover, mitogen-activated protein kinase (MAPK) is triggered due to NO generation because of ABA-mediated H_2O_2 accumulation. Thus, up-regulating genes for ROS scavenging antioxidant defense enzymes (Lu et al., 2009). ABA also plays a fundamental role in osmotic stress tolerance, as reported in ABA biosynthesis mutants of *Arabidopsis* (Koornneef et al., 1998) and other crops (Liotenberg et al., 1999) that wilt and die under prolonged exposure to drought and salt stress.

ABA-Mediated Physiological Changes Under Flooding

Flooding results in waterlogging or submergence conditions which inhibit plant growth and development. Under such unfavorable circumstances, plants always struggle to acclimatize by adapting several physiological mechanisms, including hormonal homeostasis. Change in leaf ABA concentrations in several species has been reported under waterlogged conditions (Bai et al., 2011; Salazar et al., 2015; Bashar, 2018; Cao et al., 2020). The response of ABA to waterlogging may vary among roots and leaves depending on the duration and plant species. For example, *Malus sieversii* showed more ABA concentration in the roots and leaves as compared to *Malus hupehensis* under hypoxic stress (Bai et al., 2011). According to Rodriguez-Gamir et al. (2011), the ABA level in citrus increased after 3 weeks of flooding. It was observed that the synthesis of ABA in older leaves increased and translocated to young leaves instead of ABA transportation from roots to shoots under flooding. The plant root system is severely damaged postwater logging normally in susceptible plants. Production of ROS in response to reoxygenation stress results in oxidative damage to functional tissues hampering normal physiological processes. However, a balance between CK and ABA is necessary for regulating both leaf senescence and stomatal closure under reoxygenation stages (Bashar, 2018). ABA plays a key role in modifying root hydraulic characteristics induced by asynchrony in root water uptake and leaf transpiration (Aroca et al., 2012).

The keypart of ABA is regulating the plant water balance both under flooding (Olivella et al., 2000) and drought stress (Nan et al., 2002), as detected in wheat plants. ABA concentration temporarily enhances with leaves and roots growth and then declines under water-logging conditions (Nan et al., 2002). Prolonged flooding also provokes shoot elongation, permitting the restoration of gas exchange among submerged marsh dock plant tissues and the atmosphere (Benschop et al., 2005, 2006). This adaptation procedure needs ABA-dependent biosynthesis of GA. Primarily, ethylene accumulation inhibits the expression of 9-cis-epoxycarotenoid dioxygenase, involved in downregulating ABA levels and/or activates ABA breakdown to phaseic acid (Salazar et al., 2015). The reduction in endogenous ABA is a prerequisite to stimulate gibberellin (GA) 3-oxidase expression, which is involved in translation to bioactive GA1. Downregulation of GA induced several genes encoding proteins involved in cell wall untying, during the cell cycle, interruption of starch, and other genes involved in internode development (Benschop et al., 2006). A similar response was also reported by Bailey-Serres and Voesenek (2008) in rice.

Photosynthetic capacity and carbohydrate synthesis reduced drastically due to stomatal closure resulting from enhanced ABA contents in rice leaves (Bai et al., 2013). Such kind of inhibition may also take place because of relatively greater cellular oxidative damage. Besides, ABA plays a significant role in rice adaptation to hypoxic conditions, suggesting that rice growth is tightly regulated through proline and ABA-mediated response in roots (Cao et al., 2020). Some authors also documented that the function and regulation of proline metabolism are dependent on ABA accumulation (Abraham et al., 2003). The expression of the genes involved in proline metabolism is tightly controlled by ABA-driven proline accumulation under hypoxic stress (Cao et al., 2020). Therefore, variations in gene expression linked with proline metabolism are regulated through ABA signaling, which is closely related to higher ABA-mediated antioxidant capacity in the rice roots. Under flooding stress, ABA accumulation is associated with an increase in ROS. Moreover, high ABA contents under flooding stress trigger stomatal closure and alter H_2O_2 concentration tracked by escalated antioxidant defense enzyme actions in *Arabidopsis* (Liu et al., 2012; Das and Kar, 2018). More importantly, ABA also acts as a connection between the oxidase injury of cellular structure and signal molecules under abiotic stresses through leaf senescence. However, the potential of ABA in boosting plant tolerance against waterlogging is not fully understood yet.

Ethylene Induced Physiological and Biochemical Mechanisms of Stress Tolerance

Ethylene which is a gaseous phytohormone plays a vital role in regulating numerous physiological processes including fruit ripening, flower and fruit senescence, leaf, and petal abscission (Abeles et al., 1992). Also, plants typically form increased levels of ET as a result of multiple abiotic stresses such as heat stress, waterlogging, drought, salinity, biotic stresses, organic and inorganic toxic compounds, and extreme pH. The elevated ethylene concentrations are detrimental to the plants as it triggers senescence, chlorosis, and abscission. Moreover, it has a crucial role during cell signaling for stress tolerance in several plant species. The biosynthesis and sources of ET production, interaction with other signaling molecules, and its exogenous application under different abiotic stresses have been discussed (Hussain et al., 2020).

Ethylene Mediated Physiological Changes Under Salinity

Salt-induced effects in plants are moderately attributed to the production of ET hormone (Blumwald, 2000; Mayak et al., 2004a,b; Shibli et al., 2007). This enhanced ET was detected in several plant species, like tomato (*Lycopersicon esculentum*) and *Arabidopsis* (Richard and El-Abd, 1989; Hall and Smith, 1995). Similarly, elevated ethylene, ACC content, and action of the enzyme ACC oxidase in chickpea (*Cicer arietinum*) were monitored when plants were exposed to salinity stress (Kukreja et al., 2005). The ethylene accumulation under salt stress caused physiological and biochemical modifications in hybrid tomatoes such as increased leaf epinasty, reduced growth, increased cell sap osmolarity in leaves, diminished leaf tissue viability, macro and micronutrients reduced, and altered shoot soluble protein content. However, the electrolyte leakage, membrane damage, raffinose, and total sugars were concurrently augmented (Shibli et al., 2007). Though ET inhibitors reduced ethylene accumulation and prevented epinasty, such inhibitors were unable to eradicate the negative influences on growth and other physiological limitations caused by salt stress, inferring that ET is not the major factor contributing to detrimental consequences on tomato plant development and physiology (Shibli et al., 2007). Ethylene serves as a master regulator during salinity stress and stabilizes the cell redox homeostasis, alleviating nitrate and sulfate assimilations, defense against ROS, and crosstalk with other PGRs to maintain cell signaling integrity (Riyazuddin et al., 2020). Metabolic engineering found that ethylene is an important component of phytohormone signaling and can potentially impart salinity tolerance in plants (Atia et al., 2018). Moreover, miR319 crosstalk with ET positively regulates the ET synthesis in a dose-dependent manner in switchgrass and enhances salt tolerance by downregulation of key genes of the methionine cycle (Liu Q. et al., 2019; Liu Y. et al., 2019). Therefore, several earlier findings and research suggested the role of ET in salt tolerance in many crop species by crosstalk mechanism, altering the methionine cycle, regulating the enzymes, and gene expressions.

Ethylene Mediated Physiological Changes Under Flooding

Flooding is confined to gas exchange under stagnant water, which causes expeditious assemblage of the volatile ET in all flooded plant cells. Likewise, in water-logged plants, the root is a primary organ to respond to stress and further affects the normal physiological, biochemical, and molecular functioning at the whole-plant level. Ethylene biosynthesis, signaling, and its perception under flood conditions in plants represent a step forward to develop flood resilient crop plants (Khan et al., 2020). During ethylene accumulation, the previously stored reserves are commonly used as the aerobic metabolism partly or completely stopped under flooding. This impaired the membrane integrity and the reckoning of cytotoxic compounds from the flooded soil leading to the retardation of root growth and functions. The absorption and transport of water and nutrients impaired by malfunctioned roots affect the above soil organ function, which results in wilting, senescence, and, ultimately, death of the plant. Thus, plants use some adaptive measures and/or traits such as the formation of a suberin/lignin wall (primary barrier) in the roots that keep radially of oxygen to raise its efficiency to the root tip (Shiono et al., 2011; Afzal et al., 2021), developed aerenchyma that enhances tissue absorbance and aeration of roots (Takahashi et al., 2014), and establishment of aerenchyma-rich adventitious roots (Sauter, 2013) to improve the aeration, uphold root activity and whole-plant endurance under waterlogging.

Immediate accumulation of ET is an early flooding signal and a master regulator of various waterlogging-adaptive plant measures. ACC synthase (ACS) plays a substantial role in producing ET under flooding because of hypoxia in flooded roots (Drew, 1997). The cellular fluctuations of oxygen and ET are said to be the main signals activating plant-adaptive measures to excess water, thus, the progression of distinct temporal and spatial dynamics (Voesenek and Sasidharan, 2013). The ET biosynthesis pathway is stimulated by activation of key enzymes ACC oxidase and ACS under waterlogging (Van Der Straeten et al., 2001; Lee et al., 2011; Van Veen et al., 2013). The ET biosynthesis is directly or indirectly linked to the ROS, nitrous oxide (NO), and ET cross-talk signaling and many gene expressions such as *ALCOHOL DEHYDROGENASE* (ADH), *HYPOXIA RESPONSIVE UNIVERSAL STRESS PROTEIN* (HRU1), and *ROP GUANOSINE TRIPHOSPHATASE-ACTIVATING PROTEIN4* (ROPGAP4), that regulates the hypoxia condition (Sasidharan et al., 2018). Additionally, a different subclass of ERF (ethylene response factor) is synthesized in response to multiple abiotic stress conditions. For instance, group ERF provides tolerance against flooding stress by activating hypoxia-inducible genes and regulated oxidative stress (Klay et al., 2018). Similarly, group V11 ERF *ZmEREB180* regulates flooding stress in *maize* (Yu F. et al., 2019; Yu W. et al., 2019) and *HRE2* in *Arabidopsis* (Eysholdt-Derzsó and Sauter, 2019) by promoting the emergence of adventitious roots under hypoxia conditions.

ET precursor, ACC is synthesized primarily in the roots under excess water and transported to the above-ground plant parts. There in the oxygen-mediated translation of ACC to ET occurs which results in the stimulation of the adaptive modifications *via* nastic activities and aerenchyma development in shoots (Jackson, 2002). Aerenchyma formation is species and environment-dependent and can be seen both in root and shoot organs (Colmer and Pedersen, 2008; Parlanti et al., 2011; Steffens et al., 2011), enabling plants to protrude the water surface and facilitating aeration to flooded parts. Ethylene-mediated aerenchyma formation in wheat is controlled by ROS biosynthesis by NADPH oxidases (Yamauchi et al., 2014), whereas in rice and aerenchyma, develops during normal plant life cycle exposed to a stressful environment through ET dependent manner (Takahashi et al., 2014; Yukiyoshi and Karahara, 2014). ROS is an important intermediary in the ET-mediated signaling system. For example, ET-induced development of stem aerenchyma elaborated improved levels of superoxide radicals and H_2O_2 in pre-aerenchyma cells in submerged rice internodes (Steffens et al., 2011). ROS-mediated apoptosis is the final lethal stage in the formation of aerenchyma, where the cell wall breaks down and includes ET-mediated upsurges in cellulases, pectinases, and xylanases enzymes (Bragina et al., 2003; Xu Q. T. et al., 2013). Ethylene-induced aerenchyma improves the gas diffusion between shoot and root. Although, it can entirely substitute the water-logged-roots, signaling of ET can be conflict subjected to the type of species or genotype (McDonald and Visser, 2003; Steffens et al., 2006; Vidoz et al., 2010). Ethylene-mediated aerenchyma-rich (AR) formation triggers the mechanical incentives provided by the primary root primordia that also need ethylene-mediated ROS formation (Steffens et al., 2012).

The ET-mediated hyponasty is an adaptive measure to cope with water-logged conditions with a different growth frequency of the cells that occur on the lower and upper sides of the pretentious organ (Cox et al., 2004; Polko et al., 2012). For instance, ET governs hyponasty of shoots which has been detected in *Rumex* spp. and *A. thaliana* under water-logged conditions (Cox et al., 2003; Lee et al., 2011; Rauf et al., 2013). The cross-talks between ABA, auxin, and GA with ET have been reported in response to rapid hyponasty under submergence stress (Cox et al., 2004; Benschop et al., 2006). For instance, ET-dependent elongation of the shoot is altered by combining possessions of ABA and GA under submerged conditions (Fukao and Bailey-Serres, 2008). ET regulated shoot elongation characteristics to hydrological niches and displayed two separate growth responses like escape and dormancy (Voesenek and Bailey-Serres, 2015). Flood-induced ET production is crucial for inter-nodal elongation in deepwater rice (DWR), enabling the stem to keep above the water and facilitating aeration to the whole plant (Hattori et al., 2009). It may be inferred that ET regulates the water-logging tolerance in plants by alteration in physiological, biochemical, and molecular processes and as cross-talk with other signaling components.

Ethylene Mediated Physiological Changes Under Drought

Water deficit has been connected with extended distance signaling of ACC where the elevated amount of ACC produced high levels of endogenous ET in the plants (Mayak et al., 2004a; Sobeih et al., 2004), causing growth hindrance, early senescence, abscission, and ultimately, yield penalty in important crops (Dodd, 2005). Recent molecular investigations have exposed that ABA-dependent and independent drought-inducible gene expression (Shinozaki et al., 2007). The hormone signaling pathways cross-talk under drought conditions between ABA and ethylene act antagonistically among yield-attributing components (Wilkinson et al., 2012). Ethylene is responsible for leaf abscission in plants and subsequently, checks the water loss or enhanced water use efficiency under drought situations. Aside from these, ET production leads to a subsequent drop in ACC, suggesting the rate-dependent enzyme along the pathway of ET biosynthesis (feed-back inhibition) (Apelbaum and Yang, 1981). The transport of ACC from roots to shoots in the xylem vessels demonstrates the ET evolution in leaves (Liu H. Y. et al., 2006, 2007; Liu J. et al., 2006; Liu J. H. et al., 2006). However, in such leaves, ET changes do not affect the leaf elongation in *maize* under drought (Liu H. Y. et al., 2007). This implies that long-distance sink-source signals and leaf growth inhibition under drought are associated with ET and ACC activity (Schachtman and Goodger, 2008). The ethylene inhibitor (1-MCP) induced stomatal closure showed chemically driven stomatal closure instead of hydraulic signals dependency (Sharipova et al., 2012). Increasing levels of ABA and diminishing ET levels reveals in *G. jamesonii* under water deficit, and consequently, re-watering causes the reduction in transpiration rate (Tr) and water probable of leaves (Olivella et al., 2000). Likewise, the ABA-mediated elongation of primary roots at low water potentials restricted ET production in *maize* (Spollen et al., 2000). Further, the ET production is antagonistically biased by endogenous ABA concentration during drought, controlling some drought responses in plants, e.g., root and leaf development (Tan and Thimann, 1989; Chaves et al., 2003). For instance, ABA-induced stomatal closure could antagonistically be potentially modulated by ET under drought (Wilkinson and Davies, 2009). Ethylene-induced leaf abscission in water-stressed *Citrus* plants is accompanied by ABA in roots. Thereby, providing new insights into the understanding of the mechanism of ABA and ET as primary signals under water deficit and regulation of leaf abscission (Wilkinson et al., 2012). A comprehensive understanding *via* a study of *Arabidopsis* mutant *acs7* with a lack of ET function showed the increased tolerance to multiple stresses linked to higher ABA accumulation (Dong et al., 2011). Thus, these findings suggest that the ratios of ET, ACC, and ABA regulate plant responses under water deficit conditions (Acharya and Assmann, 2009; Wilkinson and Davies, 2010; Wilkinson et al., 2012).

Ethylene Mediated Physiological Changes Under Unfavorable Environmental Variables

The ET mediates an array of physiological changes under salinity, drought, flooding, and other adverse environmental variables such as high temperature, heavy metal toxicity, etc. During heat stress, exogenous application of ethephon ($C_2H_6ClO_3P$) regulates protein metabolism, antioxidant defense, enhances pollen thermos-tolerance in tomato (Jegadeesan et al., 2018), and heat shock factor expressions in rice (Wu and Yang, 2019). Moreover, it also provides thermo-tolerance in tomato seedlings under elevated CO_2-induced heat stress *via* strengthening antioxidant defense and altering the expression of *ERF1* and heat shock factors (Pan et al., 2019). Besides, ET plays a significant part under cold stress tolerance *via* stimulating proteins related to protein metabolism, lipid stability, and antioxidant defense (Hu et al., 2017). Moreover, the *ERF057* in grapevine (Sun et al., 2016), *VaERF080,* and *VaERF087* in *Arabidopsis* (Sun et al., 2019) and *SlCBF1* in tomato (Yu F. et al., 2019) help in chilling stress tolerance. ET has a crucial role in improving the root architecture (Abozeid et al., 2017), root-shoot communications (Alves et al., 2017), regulating oxidative stress and biosynthesis, and transportation of antioxidants under oxidative stress in plants (Wang Y. et al., 2020). ET plays a key role under unfavorable environmental fluctuations and provides tolerance to plants *via* strengthening antioxidant defense, reducing oxidative stress, improved root-shoot communications, cross-talk with phytohormones, and signaling components, altering expressions of stress enzymes, genes, and proteins.

Brassinosteroids, Salicylic Acid, Nitric Oxide, Jasmonic Acid, and Strigolactones Induced Physiological and Biochemical Mechanisms of Stress Tolerance

Brassinosteroids

Brassinosteroids are a group of naturally occurring plant steroidal compounds with wide-ranging biological activity that have been given the stature of a phytohormone that offer the unique possibility of increasing crop yields through both changing plant metabolism and protecting plants from different environmental stresses (**Figure 3**). The brassinosteroids (BRs) regulate the growth and different developmental processes of plants (Yang et al., 2011; Iqbal et al., 2015). Initially, it was supposed that the BRs are physiologically related to the stimulation of stem elongation in plants (Mitchell et al., 1970; Fàbregas et al., 2018). Recently, numerous studies suggested BRs role as mediators of physiological, cellular, and molecular processes (i.e., development of anther, pollen production, stem elongation, vascular differentiation, root development, and cellulose biosynthesis) (Fàbregas et al., 2018; Javed et al., 2020). In addition, BR regulates cell division and promotes differentiation at the cellular level. Moreover, it regulates hypocotyl elongation and development of root, shoot, and leaf along with delaying senescence and reducing male sterility (Iqbal, 2015). Hence, mutants with BR impairment are observed to show short hypocotyl and petiole, delayed flowering, dark green colored leaves, reduced male fertility, dwarfism, etc. (Ye et al., 2010). There was impairment in the cell elongation with reduced parallel microtubule organization in *Arabidopsis* BR-deficient mutant, *bull-I* (Javed et al., 2020). Likewise, anomalous association and polar development of leaf and stem cells are observed in a rice mutant (BR-deficient dwarf1) that adversely affected the development of different organs (Hong et al., 2002). It was reported that BR effects largely depend on many factors including kinds of stress, plant species, growth stage, growth conditions (with or without stress), duration of stress, dose and its crosstalk with other hormones, growth regulators, and signaling molecules (Nolan et al., 2019; Yin et al., 2019).

The operation of the BR is regulated by BRASSINOSTEROID-INSENSITIVE1 (BRI1), a serine-threonine kinase plasma membrane receptor, and the inhibition of the BRI1 receptor is mediated by its C-terminal tail and inhibitor of the BRI1 kinase 1 (Wang et al., 2005; Wang and Chory, 2006). The BIN2 protein kinase is involved in the phosphorylation of the BES1/BZR1 transcription factor. It has also been found to be downstream of the BR signaling pathway (Wang et al., 2002; Yin et al., 2002). The 14-3-3 proteins are reported to hold the phosphorylated long-form of BES1 (i.e., BES1-L), BSU1, BIN2, and BES1/BZR1, and participate in the signaling of BR (Tang et al., 2008; Jiang et al., 2015). In plants, HXK1 (HEXOKINASE1) is the first known glucose sensor that induces hypocotyl elongation in darkness, mediated by BRs-dependent sugar. Thus, BR can potentially function downstream of HXK1 to regulate glucose-induced hypocotyl elongation (Zhang and He, 2015).

Brassinosteroids Related to Tolerance to Abiotic Stress

Brassinosteroid connects with other plant hormones related to stress tolerance conferring the ability of BR to play crucial roles in plant development and also advances tolerance in plants to a wide range of stresses (Ikekawa and Zhao, 1991; Ahammed et al., 2020), including heat, cold, drought, and salinity. This increase in stresses is generally correlated with higher expression of stress marker genes.

The increased expression of stress-responsive genes can be responsible for the higher stress tolerance in BR-treated plants. Several studies have confirmed the role of BRs in plant stress responses (Divi et al., 2010). The mechanisms by which BR controls plant stress responses and regulates the expression of stress response genes are not known. Fàbregas et al. (2018) showed that drought resistance is under the control of cell-type-specific BR signaling and that BRL3 overexpression activates an alternative pathway of BR signaling.

Salt Stress. The mitigation BRs of negative effects of salt stress have been shown to a wide range of plants (Ahammed et al., 2020). A study conducted by Anuradha and Rao (2001) reported that BR treated in rice seeds reduced the inhibitory effect of salt on germination. They reported the promotion of growth by BR under salt stress conditions was associated with enhanced levels of nucleic acids and soluble proteins. Although plants subjected to saline stress exhibited a reduction in all the morpho-physiological and enzymatic attributes (NRA and NiRA), proline contents and enzymatic activities of antioxidants were enhanced in response to NaCl stress. However, deleterious effects induced by salinity were reduced if seeds were treated with epibrassinolide (EBL) before or after NaCl inhibitions (Shahid et al., 2011).

In eggplants, EBR treatment-induced enhanced tolerance to salt stress is manifested by the increased activity of antioxidant enzymes, decreased Na^+ and Cl^- concentrations, and increased K^+ and Ca^{2+} concentrations. Similarly, EBR application can reduce the concentration of NO_3^- and NH_4^+ in cucumber plants under salt stress (Yuan et al., 2012). Salt stress at level 150 mM enhanced seeds germination of *Eucalyptus camaldulensis* but when seedling was grown hydroponically in salt, BR uptake through roots caused more damage (Sasse, 1999). Under salinity stress, exogenous EBR application in black locust reduced leaf Na^+ content and membrane leakage and improves the net photosynthetic rate, chlorophyll content, transpiration rate, stomatal conductance, and maximum quantum efficiency of PSII (Yue et al., 2018). When applied to a suitable concentration, brassinosteroid had a positive impact on secondary metabolite production in salt-treated peppermint (Çoban and Baydar, 2016). Ali et al. (2008) reported that EBR (1 μM) can alleviate combined stress induced by NaCl and $NiCl_2$ in Brassica juncea BR suggesting effective BRs in mitigating combined stress effects on plants. EBR applied in seed priming improves salt tolerance and induces total methylation, suggesting a role for BR in epigenetic modification under salt stress (Amraee et al., 2019).

Drought. Drought is an environmentally drastic stress that reduces crop productivity, especially in the semi-arid and arid region. In a study with cucumber plants, it was also demonstrated that BR treatment improves resistance to desiccation and high-temperature stress (Pustovoitova et al., 2001). Drought tolerance is closely associated with the accumulation of abscisic acid (ABA). Wang W. et al. (2019) showed that exogenous BR application can enhance the ABA level and mitigate the deleterious effects of drought on grapevine (*Vitis vinifera* L.) plants. In *Chorispora bungeana*, exogenous BR (0.1 μM EBR) application can enhance tolerance to drought caused by polyethene glycol (PEG) treatment (Li et al., 2011). Even *Brassica juncea* plants that experience weeklong drought stress at the early growth stage show reduced growth and photosynthetic rate even after 60 days. However, post-drought treatment with 28-homobrassinolide (HBL, 0.01 μM) at 30 days after sowing could remarkably improve both growth and photosynthesis after 60 days of sowing (Fariduddin et al., 2009). BR treatment can remarkably reduce the levels of ROS and lipid peroxidation under drought stress (Yuan et al., 2010). Although BR had a stimulatory growth effect under stress conditions when applied either as a seed treatment or foliar spray to drought-tolerant and drought-susceptible wheat varieties, overall, the drought-tolerant variety showed a higher response to BR application under water stress conditions. Increased water uptake and membrane stability and higher carbon dioxide and nitrogen assimilation rates in BR-treated plants under stress were correlated with BR-induced drought tolerance (Sairam, 1994).

Cold Stress. Low temperatures which induced chilling or freezing are considered as a handicap for plant production (Zhang et al., 2019). Cold stress-induced impairments in plants include decreased osmotic potential in the cells membrane, alterations in macromolecules activities, fluidity modifications, and also, mechanical constraints (Xiong and Zhu, 2002). In tomato (*Solanum lycopersicum* L.), mutants of BRs biosynthesis (dwf) show sensitivity to chilling stress, whereas overexpression of DWF results in an increased cold tolerance (Fang et al., 2019).

Cold stress also affects plant photosynthetic processes which are manifested by the reduction in the CO_2 assimilation rate, photoinhibition at PSI and PSII, and decreased enzyme activity (Zhang et al., 2019). Similar to heat stress, ROS can also act as signal in mediating BR-regulated responses to cold stress tolerance (Cui et al., 2011).

Cross-Talk Between BRs and Different Hormones. Brassinosteroids can increase plant resistance to a range of stresses that lies in the complex interactions of BRs with other hormones. Since different plant hormones can regulate similar physiological processes, and cross-talk between different hormones can occur at the level of hormone biosynthesis, signal transduction or gene expression, it was proposed that BR regulates plant stress responses *via* cross-talk with other hormones (Wang Y. et al., 2020). BR and ABA signaling pathways emphasize the specific regulatory mechanisms between ABA and BR responses and harmonize plant growth and development under stress. BR signaling is essential for plant development, while ABA signaling is activated to ensure plants survive stress (Bulgakov and Avramenko, 2020). BRs regulates stress adaptation through the remodeling of cell wall, induce antioxidant defense, control adventitious, and lateral root developments in plants (Rao and Dixon, 2017; Kaya et al., 2019; Betti et al., 2021). Wang Y. et al. (2020) reported that in terms of modulating plant development and stress adaptation the crosstalk between BR and ABA, especially protein phosphorylation, protein stability control and downstream transcription control of key components of both pathways.

Cross-talk between BRs and auxins, GA, ABA, ethylene, and JA includes alteration in the expression of hormone biosynthetic genes and/or signaling intermediates (Finkelstein, 2013). The roles of ABA in cold, salt, and drought stresses (Zhu, 2002), and those of JA and ethylene in plant defense responses (Wang et al., 2002) are well-documented, the involvement of these hormones in BR-mediated stress tolerance with their crosstalk.

Salicylic Acid

Salicylic acid alleviates the adverse impacts of numerous abiotic stresses. For instance, the activities and levels of enzymes involved in the biosynthesis of SA are observed to be enhanced under salt stress in rice plants (Sawada et al., 2006; Hoque et al., 2020a,b). SA, itself, facilitated the restoration of membrane potential and averted the salinity stress persuaded K^+ loss *via* GORK channel in *A. thaliana* (Jayakannan et al., 2013). The SA enhanced salinity resistance in barley *via* an increase in the Chl and carotenoid contents and sustained membrane integrity by accumulating K^+ and soluble sugars (El-Tayeb, 2005). The SA regulated the photosynthetic process under salinity stress in mung bean cultivars by increasing the assimilation of nitrogen and sulfur, along with antioxidant metabolism (Nazar et al., 2011). Thus, both BRs and SA are well-avowed to advance stress tolerance by mitigating the harmful effects of abiotic stresses, especially salinity stress in plants (Ashraf et al., 2010; Bali et al., 2017).

Nitric Oxide

It is a volatile gasotransmitter having key functions as a regulator of vital plant growth processes *viz*., seed germination, root growth, floral transition, pollen tube growth, fruit ripening, photosynthesis, mitochondrial functionality, senescence, seed dormancy, gravitropism, stomatal movements, etc. (Siddiqui et al., 2011; Manai et al., 2014; Mostofa et al., 2015). Recently studies suggested that has crucial role during regulation of signaling network under normal and stress conditions, post-translational modifications, and regulation of oxidative stress through activation of antioxidant defense system (Sami et al., 2018; Sharma et al., 2020). NO cross-talk with other PGRs and regulate the fundamental processes under stress situations (Kumar and Pathak, 2018). Under drought stress, NO mediates the water status and associated enzymes to inhibit nutrient balance, oxidative defense, and primary and secondary metabolism, (Akram et al., 2017; Majeed et al., 2020; Wang X. et al., 2020). Under salinity stress, the endogenous supply of NO improved plant growth and increased osmotic pressure and cytoplasmic viscosity of plant cells (Dong et al., 2014). NO alleviates stress effects by mediating plant responses through upregulation of antioxidant defense system mediated by SA and H_2O_2 (Klessig et al., 2000; Mostofa et al., 2015; Singh et al., 2015).

Jasmonic Acid

Jasmonic acid and methyl jasmonates (MeJA) play a key part in improving plant stress tolerance *via* improving plant growth and physiological activities (i.e., reproductive processes, sex determination, fruit ripening, the formation of storage organ, senescence, interaction with other hormones, etc.) (Avanci et al., 2010; Cipollini, 2010; Nafie et al., 2011). Furthermore, being involved in chlorosis, antioxidant enzyme upregulation, senescence, seed and flower growth, and systemic resistance leads to protection against environmental stresses (Creelman and Mullet, 1997; Seltmann et al., 2010; Soares et al., 2010; Pieterse et al., 2012; Wasternack et al., 2012).

Strigolactones

Strigolactones are carotenoid-derived phytohormones that were first identified as germination stimulant in parasitic weeds and creating plant-microbe symbiotic relationship (Xie et al., 2010). Subsequently, strigolactone (SL) role in regulating the hyphal branching in the symbiotic association between plants and arbuscular mycorrhizal fungi (AMF) has also been reported (Akiyama et al., 2005). Furthermore, characterization of SLs have showed functional roles in root and shoot development, photomorphogenesis, leaf senescence, flower development, and suppression of shoot branching (Gomez-Roldan et al., 2008; Waters et al., 2017). The SLs have drawn special attention due to their physiological and molecular regulatory processes against various abiotic stresses. SL modulated stress responses through ABA was reported in *Arabidopsis*, where SL positively regulate stomatal closure (Ha et al., 2013). Contrary, cytokinin was found to negatively regulate the same process (Nishiyama et al., 2011). SL-loss of function mutants showed dense lateral root growth and inhibit adventitious root formation in many plant species (Arite et al., 2012; Rasmussen et al., 2013; Urquhart et al., 2015). Moreover, SL-deficient mutants are susceptible to water deficit and salt stresses inferring positive regulatory mechanisms in stress acclimatization (Cardinale et al., 2018). The SL modulated biological processes against environmental stresses are complex. This complexity is clearly reflected by the collective functions of abscisic acid, cytokinin, and SL in stomatal regulation and leaf senescence for plant adaptation to adverse environments (Lim et al., 2007; Czarnecki et al., 2013). Thus, these studies provide evidence to cross talks between SL and other phytohormones in response to adverse environments.

EXOGENOUS APPLICATION OF PLANT HORMONES TO SUPPORT STRESS RESISTANCE IN PLANTS

Through exogenous supplementation of natural and synthetic PGRs, negative consequences of abiotic stress can be mitigated to a greater extent, although not completely. The PGRs like GA, ABA, and CK are applied solely or in combination to improve plant stress tolerance. The application of these hormones (GA_3, ABA, and CK) showed a higher grain yield when applied by foliar spraying to dry seeded rice genotypes. They also increased the number of filled grains per panicle, thereby improved the harvest index. Moreover, GA_3, ABA, and CK also increased the activities of antioxidative enzymes (superoxide dismutase:SOD, and peroxide dismutase:POD) as a defense strategy against different altered soil moisture regimes (Rajinder et al., 2020). According to the report of Leshem et al. (1981), senescence can be delayed by the supplementation of GA_3 at the grain filling stage. Whereas, the exogenous supply of ABA is observed to enhance the moisture stress resistance in plants (Wang et al., 2003; Li et al., 2004).

A reboot of drought-induced low plant growth could be achieved through the exogenous application of CK *via* improving photosynthesis, water use efficiency, and antioxidant metabolism of shoots (Kudoyarova et al., 2007; Ghanem et al., 2011; Merewitz et al., 2011; Nishiyama et al., 2011). CK protects plants under stressed environments from oxidative damage *vis* modulating the actions of antioxidants, particularly of CAT, SOD, and POD (Synkova et al., 2006; Zavaleta-Mancera et al., 2007; Zhang et al., 2008). An enhancement in the tiller production of cereals (barley, oat, and wheat) was observed in response to foliar application of SS-ethephon chlormequat chloride (CCC), a form of ethylene and trinexapac-ethyl and (TE) under stress. However, they remained ineffective in boosting shoot growth (Rajala and Peltonen-Sainio, 2001).

Exogenous SA application is reported to be positively connected with enhanced tolerance of plants to different abiotic stresses *via* stimulating the activity of antioxidant defense enzymes (Kaydan et al., 2007; Ashraf et al., 2010). Furthermore, SA plays numerous essential roles in photosynthetic rate, stomatal conductance, transpiration, switching antioxidative defense system and inhibiting Na^+, and Cl^- accumulation (Arfan et al., 2007; Gunes et al., 2007; Xu et al., 2008; Fayez and Bazaid, 2014). In the work of Jafar et al. (2012), the supply of SA improved the overall yield of two wheat cultivars grown under salinity stress. Foliar application of SA can decrease the contrary effects of salt stress by helping seedling growth, reinstating plant growth, and supporting the uptake of proline, ABA, indole IAA, and CKs. Foliar application of phytohormones like auxin, IAA, CK, and BR showed stress alleviated stress by improving the antioxidant enzymes activities (SOD, POX, APX, and GPX) and accumulating the non-enzymatic antioxidants (tocopherol, ascorbate, and reduced GSH) (El-Mashad and Mohamed, 2012). The exogenous application of BRs and SA regulated different biochemical and physiological procedures to increase salt resistance in crop plants (Ashraf et al., 2010).

Exogenous applications of JA and MeJA created resilience in plants against stressful growth factors and adverse environments. For example, JA protected *Zucchini* against chilling stress, whereas in *Mangifera indica*, the treatment of MeJA enhanced fruit quality and improved chilling tolerance (Wang and Buta, 1994; Gonzalez-Aguilar et al., 2000). In other edible plants, the treatment of MeJA reduced the fungal development in grapefruit and upheld the post-harvest quality of papayas (Droby et al., 1999; Gonzalez-Aguilar et al., 2003). In addition, JA and MeJA, when supplemented exogenously to raspberry, have improved fruit quality *via* switching the antioxidant system (Ghasemnezhad and Javaherdashti, 2008; Wang K. et al., 2009). The process of germination was observed to be kindled in the dormant seeds with the exogenous applications of MeJA and JA (Ranjan and Lewak, 1992; Norastehnia et al., 2007; Dave et al., 2011). The application of MeJA and JA promoted essential oil biosynthesis in various oil crops (Rodriguez-Saona et al., 2001; Zhang et al., 2005). Thus, NO, ROS, calcium, ABA, ET, and SA together act as vital mediators of plant growth and development during JA signal transduction and synthesis.

CONCLUSION

Globally, the individual or combined effect of different abiotic stresses is seriously reducing the biological and economical yields of numerous crops which necessitates the development of biologically viable strategies to cope with these stresses. Endogenous biosynthesis of PGRs and their exogenous application as seed priming or foliar agents have the potential to mitigate the adverse impacts of abiotic stresses. The various types of PGRs interrelate with complex signaling systems to equilibrate the responses and thereby overcome damages caused by stress environmental conditions. Plants have developed complex mechanisms governed by multiple receptors to receive external signals and subsequently trigger an optimal response against stress conditions *via* PGRs that mainly control the defensive responses of plants by synergistic and antagonistic activities which has been referred to as signaling cross-talk. The interaction of phytohormones and stress is a well-known event in plant stress management. The list of these candidates involves both the classical and newly discovered phytohormones, and the list is continually growing with the advent of novel growth stimulatory phytochemicals. However, there is a dire need to investigate various factors which trigger the biosynthesis of PGRs in crop plants along their transportation receptors to increase our understanding of PGRs ameliorative role in stressed plants. Moreover, PGRs play a key role in association with crop growth stage, along with intensity and duration of abiotic stress, and need to be investigated in different crop species. PGRs signaling is very complex and at multilevel, affects the plant growth and developments. Therefore, the deep molecular understanding of plant hormone receptors, and ligands under multiple stresses can help to develop multiple stress tolerant crops. Likewise, the responses of plant hormone are modulated according to situations as singular stress or multiple stress. Therefore, the hormonal response under various stages and various stress factors are very crucial to understand the complex mechanism of abiotic stress tolerance. Moreover, the novel plant growth regulators such as salicylic acid, nitric oxide, strigolactones, and other signaling compounds have fundamental roles in regulating the stress and hormone response, which could be more focused in the near future to understand the crosstalk network of cell signaling. Consequently, in the recent years, various transcription factors such as MYB, MADS, WRKY, and NAC had crucial roles in plant growth and development and also respond to multiple abiotic stresses regulated by PGRs, having future hopes to develop stress tolerant transgenics.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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