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Abiotic Stress Tolerance in Crop Plants: Role of Phytohormones

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Abstract

Crop plants are encountered by various abiotic pressures which limit their growth and development. Stresses such as drought, heat, pathogen attack, heavy metal, salinity, and radiations impose negative effect on crop plants. The reduction in crop productivity in the current era of climate change is compromising the efforts/strategies used for sustainable agricultural practices. Therefore, plant stress physiologists are engineering plants with suitable exogenous signaling elicitors to engineer tolerance to various stresses. In the present chapter, an appraisal has been made in the “Introduction” section to first assess the damages caused by various abiotic stresses in crop plants. In the second section, we attempt to summarize the role of various plant hormones, namely, salicylic acid (SA), brassinosteroids (BRs), ethylene (ET), and methyl jasmonate (MJ) in enhancing abiotic stress tolerance. The current concept may lead to the development of strategies for unraveling the underlying mechanisms of plant hormone-mediated abiotic stress tolerance in crop plants.

Keywords: abiotic stress, plant hormones, crop plants, stress tolerance

1. Introduction

Due to overexploitation of natural resources for catering to basic human needs coupled with hunger, the aim of Food and Agricultural Organization’s [1] of making world agriculture for enhancing 70% food production by 2050 for 2.3 billion newborn individual is facing a lot of challenges. As a result of changing climate and global warming, these threats are now called as “global warning” due to their effects on plant productivity [2]. According to a report published by IPCC [3], global climate change will increase the mean temperature of the Earth by 2–4°C. Due to increased anthropogenic activities, the change in climate will further increase and will definitely affect the agriculture sector as this is being more prone to climate changes [4]. A change in climate scenarios is the main reason of biotic and abiotic pressures of a particular region. Various abiotic stresses all over the world have now been adjudged as the most potential threat for sustainable agricultural productivity [5, 6]. Myriads of anthropogenic emissions in the developmental era have further intensified the abiotic stress-induced negative impacts on agricultural productivity. The major abiotic stresses such as metals/metalloids (hereafter termed as “metal/s”), salt, ozone, UV-B radiation, temperature extremes, nutrient (deficiency and excess), flooding, and water deficit are jeopardizing the agriculture system

worldwide [7–19]. These abiotic stresses can modulate almost all plant physiological, biochemical, and molecular processes starting from the seedling to maturity stage and can ultimately cause severe negative impacts on economic yield of various crop plants. Nevertheless, abiotic stresses have been reported to adversely affect 70% yield of crops [20]. The stress of metal/s is known to affect the photosynthetic process to a great extent [19, 21]. According to an estimate of U.S. Environmental Action Group, various metals pose negative effects on health in more than 10 million of human population in eight countries (such as China, India, Russia, Dominican Republic, Kyrgyzstan, Peru, Ukraine, and Zambia) and the effect imposed by them is regarded as one of the major threats to the agriculture [22]. Wang et al. [23] have reports to show that the salinization of arable land could accelerate to a land loss of 30% by the year end of 2028 and up to 50% by 2050. In current times, an increase in atmospheric CO₂ concentration has been reported to reach by 407.4 ppm, and its levels today are more than at any point recorded for at least the past 800,000 years [24]. In addition, the data accessed on NOAA website [25] show that the average global temperature in June 2020 was found to be 1.66 °F (0.92 of a °C) above the twentieth century's average of 59.9 °F (15.5 °C) and the average temperature of June across the U.S. was found to be 70.3 °F (which is 1.8° above average), which ranks it the warmest third month in the history of the 126-year record. Hence, all these abiotic stress factors under the effect of climate change could be expected to significantly pose a potential threat to agriculture [11, 26–30]. Therefore, the knowledge of crop productivity improvement techniques under various abiotic stresses is one of the biggest challenges encountered by the scientific community across the world. Despite much and extensive efforts being utilized in the current field, the underlying quest for obtaining abiotic stress-resistant crops is very low and receives little attention. Various efforts are being utilized to decipher the potential mechanisms behind plant responses to abiotic stress conditions. Plants are sessile and are exposed to various environmental regimes and have to tolerate these abiotic stress-induced adverse impacts for performing their growth and development in an optimal manner. As a result of an exponential increase in the global human population, the demand for enhanced food is also accelerating and in order to meet these challenges under a challenging environment, it has become necessary to increase crop productivity. Nevertheless, the exogenous use of phytohormones in these adaptive mechanisms for engineering abiotic stress tolerance in diverse crop plants can yield better results.

Phytohormones are small chemicals messengers that play important roles in regulating the promotion of growth, development, and metabolism of the plants in a wide range of biotic and abiotic stresses. These are biodegradable and highly promote the growth and crop yield under optimal as well as stressed conditions. The knowledge of engineering in plants could be exploited to impart tolerance against a wide range of abiotic stresses. Thus, the present chapter focuses on the potent role of various phytohormones in enhancing the morphological and physiological properties of crop plants and also sheds light on the alleviative role in providing plant tolerance to various environmental stresses.

2. Regulatory role played by various phytohormones in abiotic stress tolerance in crop plants

In the following sections, we will be discussing the potential role of different phytohormones like SA-, BRs-, ET- and MJ-mediated mechanisms in countering diverse abiotic pressures like salinity, drought, heat, and metal/s stress in diverse crop species. The role of these phytohormones in eliciting various responses in different crop plants has also been represented in **Table 1**.

Name of plant	Abiotic stress, type, and doses	Phytohormone doses	Consequent response	Reference
<i>Mentha arvensis</i> L.	Metal stress Cd (150 mg/Kg)	Methyl jasmonate 1 μ M	A significant decrease in length of root and shoot, fresh and dry masses of shoot and leaf area; decreased chlorophyll and leaf gas exchange traits, and leaf N, P, and K content; increase in the activities of APX, GR, SOD, CAT, ROS production, osmolytes; and closure in stomatal movement under Cd. Improvement in these traits and alleviation of stress by MJ application	Zaid and Mohammad [31]
<i>Mentha piperita</i>	Cd 30, 60, and 120 mg/kg	Salicylic acid 10^{-4} M	Decreased growth and photosynthetic traits and enzymes like NR and CA activities; increased phenolics, activities of SOD, POX, and proline content under Cd. SA improved photosynthesis; activity of RuBisCo, CA, and GSH pool, EO content; and yield of peppermint plants	Ahmad et al. [32]
<i>Glycine max</i> L.	Salt 100 mM	24-epibrassinolide 10^{-7} M	EBL application decreased Na^+ accumulation and promoted the uptake of the mineral nutrients, modulated osmolytes, activities of key antioxidant enzymes, and the levels of nonenzymatic antioxidants thus improves growth and photosynthesis	Alam et al. [33].
<i>Linum usitatissimum</i>	Salt 150 mM	24-epibrassinolide 10^{-8} M	NaCl decreased methylation of CCGG sequences. EBL application induced the total methylation under salinity stress conditions	Amraee et al. [34].
<i>Brassica juncea</i>	Cr 1.2 mM	200 μ L/L ethephon application	ET was found to be involved in reversal of Cr-inhibited growth and photosynthesis by increasing PSII efficiency and enhanced N and S assimilation	Asgher et al. [35]
<i>Brassica juncea</i> L.	As 50 and 200 μ M	Methyl jasmonate 0.1 and 1.00 μ M	MJ application effectively mitigated the adverse effects of As stress by increasing the biomass, chlorophyll fluorescence, and the biosynthesis of secondary metabolites, reducing the oxidative stress biomarkers and maintaining antioxidant system	Farooq et al. [36]
<i>Phaseolus coccineus</i>	Metal stress Cu (50 μ M)	Methyl jasmonate 10 μ M	The enzymatic activities SOD, CAT, APX, POX, as well as MDA, GSH, and proline increased under Cu stress. MJ also elevated the activities CAT, APX, and POX activities in the roots. Final results showed that MJ was partially effective in modulating the anti-oxidative enzymes' activities and accumulation of metabolites, in both normal and Cu-stressed plants	Hanaka et al. [37]

Name of plant	Abiotic stress, type, and doses	Phytohormone doses	Consequent response	Reference
<i>Mentha piperita</i>	Salt (0, 50, 100, or 150 mM NaCl)	Salicylic acid, gibberellic acid, and triacontanol, each with 10^{-6} M	The salinity stress decreased growth, photosynthesis, activity of CA, contents of N, P, K, peltate glandular trichome density, EO and menthol content, and herbage yield but increased CAT, POX, and SOD activities and proline. The foliar spray of SA surpassed the other two phytohormones and maximally improved all parameters under both salt stress and salt free conditions	Khanam and Mohammad [38]
<i>Brassica juncea</i>	Ni 200 mg/kg	Ethylene 200 μ L/L	The results showed that Ni decreased growth and photosynthesis but increased oxidative stress. Supply of ET ameliorated the stress by increasing the proline synthesis, antioxidant defense, and glyoxalase systems to promote the photosynthetic effectiveness under Ni stress	Khan et al. [39]
<i>Artemisia annua</i>	Metalloid stress (Boron) 1.00 and 2.00 mM	Methyl jasmonate 300 μ M	B decreased the stem height, fresh and dry masses of the plant, the net photosynthetic rate, stomatal conductance, internal CO ₂ concentration, and total chlorophyll content. MJ supply alleviates changes in growth and photosynthetic efficiency by increasing the activities of antioxidant enzymes and yield of secondary metabolites	Aftab et al. [40]

Table 1.

Various studies in diverse crop plants under different abiotic stresses conditions and the consequent response shown by these plants under various phytohormone application.

3. Role of salicylic acid

The name of “salicylic acid SA” is known to be derived from the Latin word *Salix* (willow tree). A German scientist, namely, Johann Andreas Buchner in 1828, isolated a quantity of glucoside of salicylic alcohol “salicin.” Later on it was found that salicin, an important salicylate, is present in 36 other plants in addition to willow tree [41]. Chemically, SA is a simple phenolic compound ($C_7H_6O_3$) and consists of an aromatic ring to which one carboxylic and a hydroxyl group are attached. SA participates in several important plant processes either in stress-free or stressful environmental cues. It is now regarded as an important protector and growth regulating molecules in plants [42]. SA has an evidenced role in improving abiotic stress tolerance in various crop plants. Nonetheless, a report by Li et al. [43] suggested that SA acts upstream of NO under high concentration of carbon dioxide (CO_2) to induce enhanced flavonoid biosynthesis in tea plants. The results advocated the cross talk of SA for enhanced biosynthesis of secondary metabolites in tea plants under the era of climate change. In watermelon plants, resistance against root-knot nematode by red light is regulated by the coordination of SA with jasmonate signaling. This shows the potentiality of SA in enhancing tolerance against biotic stress. In Indian mustard plants, SA (10^{-5} M) alleviated the toxicity of Ni (50, 100 and 150 μ M) by upregulating the activities of enzymes associated with antioxidant defense and glyoxalase systems [44]. In yet a recent study, Zaid et al. [45] tested the efficacy of foliar supplementation of SA (10^{-6} M) in two menthol mint cultivars, namely, Kosi and Kushal grown under Cd (50 μ M) stress conditions. A reduction in growth, photosynthesis, and mineral nutrients with a concomitant increase in electrolyte leakage (EL), malondialdehyde (MDA), and hydrogen peroxide (H_2O_2) contents was observed under Cd stress in both cultivars. Nevertheless, a differential upregulation of proline content and the activities of antioxidant enzymes under Cd stress were also noticed in both cultivars. In contrast, out of three foliar-applied PGRs, the application of SA at three different growth stages proved best in alleviating Cd toxicity that too in both the cultivars but the effect of SA in Kushal was much more pronounced and better than Kosi. Application of SA (10^{-6} and 10^{-5} M) was also found to restrain As toxicity in two varieties of *Artemisia annua* L., namely, “CIM-Arogya” and “Jeevan Raksha” at 90 and 120 days after plantation [46]. The results suggested that the minimum reduction in growth and yield occurs with enhanced artemisinin production in “CIM Arogya” compared to “Jeevan Raksha” under As toxicity (45 $mg\ kg^{-1}$ of soil). The application of SA via leaf significantly increased the content and yield of artemisinin in both varieties. El Dakak and Hassan [47] in a study evaluated the underlying physiological and biochemical mechanisms through which SA (1.0 mM) applied as a soil drench treatment alleviated the toxicity of Cd (5 and 10 μ M) in maize plants. The results showed that exposure of maize plants to Cd reduced the chlorophyll content, chlorophyll fluorescence traits, photosynthesis, and catalase (CAT) activity, but, however, enhanced non-photochemical quenching (NPQ), MDA content and activities of superoxide dismutase (SOD), ascorbate peroxidase (APX) and guaiacol peroxidase (GPOX). Application of SA through soil drenching had an additive effect on the activities of antioxidant enzymes, but an inverse effect was found in case of MDA content. Es-sbihi et al. [48] studied the effects of SA (0.5 and 1 mM) on physiological traits, distribution of glandular hairs and essential oil (EO) composition in *Salvia officinalis* L. grown under Cu contamination (40 mM). The Cu stress decreased the growth of stem and root, Ca, P and K content in leaves as well as in roots. Interestingly, Cu increased EO yield. SA spray more prominently at 0.5 mM significantly improved stem and root growth, Ca, P, K and EO content and increased the density of peltate glands in presence of Cu stress. The study concluded with the observation that foliar

spray of SA showed the remediating effect on growth traits, biosynthesis, and composition of EO of *S. officinalis* plants grown under Cu-challenged environment. This shows the key role of SA in enhancing tolerance to metal stress. In case of salt stress, SA also plays a mitigating role in minimizing the salt-induced damages in diverse crop plants. Miao et al. [49] in a hydroponic study applied exogenous SA (0.3 mM) in alleviating salt stress (50 mM NaCl) in cucumber seedlings. The results showed that 50 mM NaCl toxicity reduced relative growth rate and leaf photosynthetic traits like Fv/Fm, Φ II, and Pn. However, plants receiving NaCl + SA treatment showed a significant increment in relative growth rate, leaf photosynthetic traits (mentioned above) and an increase in case of total root length, root surface area, number and total lengths of primary and secondary roots. Both NaCl and SA downregulated and upregulated the expression of *GL2* and *RHD2* gene expression, while the application of SA treatment to NaCl-treated plants showed a notable upregulation in the expression of *NAC1*, *NAC2*, *GL2*, *EXP*, and downregulation of *RHD2* gene expression. Taken together the exogenous application of SA alleviated the NaCl toxicity by enhancing photosynthesis and architecture of root system in cucumber seedlings. Hussain et al. [50, 51] worked out the mechanistic elucidation of SA (0.5 mM) interplay with S (2.0 mM) under salt stress (50 mM NaCl) in mung bean plants. Salt-exposed plants showed an elevation in reactive oxygen species (ROS) content, lipid peroxidation, glucose and enzymatic activities like APX, GR, SOD, and reduced glutathione (GSH) and proline but marked inhibitions in the nitrate reductase (NR) and nitrite reductase (NiR) activities, N content, photosynthesis, photosynthetic N-use-efficiency (NUE), and growth traits. The supplementation of SA and S strengthened the antioxidant machinery, improved NR and NiR activities, N content, GSH, APX, GR and also decrease in ROS, MDA and glucose (a photosynthesis repressor) accumulation. These observations suggested that fine-tuning of SA with S diminished the NaCl-mediated changes in tested plants. Fahad and Bano [52] investigated the effect of foliar spray of SA (10^{-5} M) on maize (*Zea mays* L.) hybrid cv. 3025 grown in saline environments (pH 8.4 and EC 4.2 ds/m). The salinity treatment was found to significantly increased sugar contents, protein, proline, and activities of SOD, POD, CAT, and APX but decreased the pigment contents like chlorophyll and carotenoid and osmotic potential and membrane stability index. The application of SA to plants grown under salt-stressed plants further incremented the osmolytes, antioxidant enzymes, contents of endogenous abscisic acid (ABA), indole acetic acid (IAA), root length, and fresh and dry weights of roots. The results indicated that foliar application of SA proved to be effective in ameliorating the ill effects of salinity stress on maize plants. Pan et al. [53] worked out the involvement of hydrogen sulfide (H_2S) in SA-induced chilling stress tolerance in cucumber seedlings by using specific scavenger and inhibitor of H_2S . They found that under optimal conditions, the donor of H_2S or removing of endogenous H_2S by its scavenger (hypotaurine) or inhibitor (DL-propargylglycine) showed no impact on the level of endogenous SA, but SA induced H_2S endogenously and triggered the activities and mRNA transcript levels of L-/D-cysteine desulphydrase (L-/D-CD). In addition, inhibiting endogenous SA with paclobutrazol or 2-aminoindan-2-phosphonic acid inhibited the effects of SA on H_2S . Nevertheless, both SA and H_2S donor NaHS minimized chilling-induced injury by lowering EL, MDA content, and ROS accumulation, improving the activities and mRNA levels of SOD, POD, CAT, APX, and GR, contents of ascorbate (AsA) and GSH contents and enhanced the expression of the chilling responsive genes (*ICE*, *CBF1*, and *COR*). It was postulated from this study that SA acts as an up-streaming signaling molecule under chilling tolerance of cucumber plants via increasing antioxidant defense system and modulating the expression of chilling stress-responsive genes. In a comparative study involving three deficit irrigation regimes, viz., 100, 80, and 60%

of crop evapo-transpiration and four levels of salinity, that is, 2, 4, 8, and 12 dS m⁻¹, the effect of SA in pearl millet and wheat plants was studied [54, 55]. Water and salinity stress caused significant reductions in grain yields, plant height, water and proline content, and Fv/Fm and Na/K⁺ ratios in both pearl millet and wheat plants. Supply of SA caused a significant enhancement in plant height and grain yield and significantly improved all physiological, biochemical traits and consequently grain yield in both crop plants. In order to evaluate the participation of NR in SA-mediated improvements in water deficit tolerance in pepper plants, Kaya [56] applied 0.5 mM SA as a foliar spray. The results revealed that water stress caused decrement in total plant dry weight, Fv/Fm, contents of chlorophyll *a* and *b*, relative water content, leaf water potential but increment in MDA, H₂O₂, EL, methylglyoxal (MG), proline, and (nitric oxide) NO, NR and antioxidant enzymes' activities. The supply of SA reduced oxidative stress biomarkers, but triggered a marked increment in antioxidant defense system, enzymes of ascorbate-glutathione (AsA-GSH) cycle and glyoxalase system-glyoxalase I (Gly I) and glyoxalase II (Gly II), growth and photosynthetic traits, activities of NO, NR and proline content. In a recent study, the effect of foliar SA (0, 0.5, and 1 mM) under drought stress (90, 60, and 30% field capacity) in *Portulaca oleracea* L. was studied [57]. Imposition of drought stress showed a decrement in the contents of photosynthetic pigments, gas exchanges attributes, growth, and biomass production, soluble sugars, total phenolic, flavonoids and unsaturated fatty acids (FA) like oleic, linoleic and linolenic acid, and stearic and behenic acid but increased the contents of H₂O₂, MDA, and palmitic and arachidonic acid, respectively. Application of SA improved the growth, photosynthetic pigment contents, gas exchanges traits, FA contents, compatible solutes, and secondary metabolites, while simultaneously decreasing drought-induced oxidative stress biomarkers. With regard to heat stress, SA is effective in alleviating the damages on plants' physiology. Karpets et al. [58] studied the interplay of hydrogen sulfide (H₂S) in SA-mediated induction of heat resistance via the performance of antioxidant system in wheat plantlets. The data showed that H₂S actively participates under the protective influence of SA application in wheat heat stress tolerance. Khan et al. [59] exposed wheat plants to heat stress (40°C for 6 h) and studied the potential of 0.5 mM SA in alleviating the negative effects of heat stress on photosynthesis. The net photosynthesis (Pn) and activity of ribulose 1,5-bisphosphate carboxylase (RuBisCo) and photosynthetic nitrogen use efficiency (NUE) decreased under heat stress, but metabolism of proline was found to be increased. The application of SA alleviated heat stress by further increasing proline metabolism via the enhancement in the activity of γ -glutamyl kinase (GK) and decrement in proline oxidase (PROX), which maintained optimum osmotic and water potential for optimally maintaining the photosynthesis. Nonetheless, SA restricted the production of stress ethylene under heat-stressed plants to optimal range. The results suggested that SA supplementation alleviates heat stress effects by interacting with proline metabolism and ethylene formation to improve photosynthesis in wheat plants. In yet another related work, Kumar et al. [60] by using MALDI-TOF-TOF/MS analysis showed that spraying 100 mM SA alleviates the heat-induced (38°C) oxidative stress damage in wheat plants via modulation of the expression of heat-stable genes and proteins. Thus, SA application plays a pivotal role in alleviation the damages of myriads of abiotic stress in diverse crop plants.

4. Role of brassinosteroids

Brassinosteroids (BRs) are an important class of plant steroid-based phytohormone that plays multiple roles in regulating plant growth, development, and

responses to environmental stresses [7, 8, 50, 51, 61–64]. 28-homobrassinolide (HBL) and 24-epibrassinolide (EBL) are the two isomers of BRs which regulate an array of plant physiological processes [65, 66]. BRs have structural resemblance with androgens, estrogens, corticoids, and ecdysteroids. The discovery of brassinolide (BL) dates back to 1979, and now about 70 compounds which are naturally occurring have been reported as free molecules or form conjugates with glucose and FA [67]. The isomers of BRs play a significant role in imparting abiotic stress tolerance in crop plants. In potato plants, Kolomeichuk et al. [68] studied the EBL-mediated (10^{-10} M) alleviation of NaCl toxicity (root application 100 mM) on photosynthetic processes. Salinity inhibited the contents of photosynthetic pigments, photosynthetic electron transport and photosystem II (PSII) maximal and effective quantum yields, oxidation of the plastoquinone (PQ). The treatment with 24-EBL under salinity stress maintained the efficiency of PSII photochemistry, PQ pool oxidation, and decrease in leaf osmotic potential. Amraee et al. [34] reported the 24-EBL-mediated (10^{-8} M) alteration on the extent and pattern of DNA cytosine methylation in *Linum usitatissimum* L. plants under salinity stress (150 mM) by using methylation-sensitive amplified polymorphisms (MSAP) technique. In conclusion, they found that the seed priming with 24-EBL play an important regulatory role via the epigenetic modification and induction of methylation in response to salinity toxicity. 24-EBL (10^{-8} mM) also confers tolerance against NaCl (100 mM) stress in soybean plants [33]. Exposure of soybean plants to 100 mM salt stress decreased growth, biomass yield, gas exchange traits, photosynthetic pigment contents, and chlorophyll fluorescence but increased H_2O_2 , MDA, EL, and the antioxidant activities like SOD, CAT, accumulation of proline, and glycinebetaine (GB), total phenols, and total flavonoids. Application of 24-EBL (10^{-8} mM) to salt-stressed plants' upregulated the growth, biomass, yield, gas exchange and photosynthetic pigment contents, and chlorophyll fluorescence parameters but concomitantly reduced the accumulation of oxidative stress biomarkers. In a factorial experiment, Kaya et al. [69] studied the effect of 24-EBL (1.5 and 2.0 μ M) application in regulating key physio-biochemical traits and oxidative defense system in two cultivars of maize, namely, PR32T83 and PR34N24 under two salinity levels (1.1 and 8.0 dS/m). Salinity levels decreased the fresh and dry weights of plant, yield of PS-II, chlorophyll contents, leaf water potential, and leaf K and Ca levels, but triggered an increase in membrane permeability, lipid peroxidation, H_2O_2 , SOD, POD, CAT enzymes' activities, leaf Na and Cl, proline and GB, and leaf sap osmotic pressure. However, 24-EBL supply via both seed treatment and foliar application to the maize cultivars alleviated the detrimental effects of salt stress. In *Cucumis sativus* L. cv. Jinyan No. 4, plants grown under vermiculite and in hydroponic culture, Ahammed et al. [70] tested the efficacy of 24-EBL in alleviating organic pollutants (OPs), namely, 2,4,6-trichlorophenol, chlorpyrifos and oxytetracycline-retarded root elongation by unraveling the redox homeostasis and secondary metabolism-mediated underlying mechanisms. The results revealed that all the three tested OPs retarded elongation of roots, increased MDA, H_2O_2 and NO, while exogenous 24-EBL markedly decreased the accumulations of H_2O_2 , NO and MDA *vis-a-vis* upregulating the expression of genes associated with antioxidant and detoxification systems. In case of pesticide stress, 24-EBL maintained the optimum synthesis of proteins and amino acids in *Brassica juncea* L. plants [71]. They applied 24-EBL (100 nM) via the seed presoaking treatment to study the changes in the synthesis of protein and amino acid contents grown under im-idacloprid (IMI)-challenged environment. Plants grown under IMI stress (300 mg/kg soil) showed a decrease in protein and 21 amino acid contents. However, application of 24-EBL restored the total protein as well as amino acid contents which was decreased under IMI amended soils. In a recent study laid out in a randomized block design under

greenhouse, Jan et al. [72] applied 24-EBL (10^{-7} M) for 8 h as seed priming method to alleviate the toxic effects of Cr (10 mg/kg soil) in tomato plants. The results suggested that that 24-EBL application effectively stimulate growth of tomato plants exposed to Cr stress via the remodulation of the physiological, metabolic, and defense mechanisms and by maintained accumulation of Cr. Alam et al. [33] applied 24-EBL (10^{-7} M) in countering NaCl (100 mM) stress in soybean plants. Salinity decreased growth, gas exchange parameters, pigment contents, and chlorophyll fluorescence, Ca^{2+} , K^+ , and P and biomass yield but H_2O_2 , MDA, EL, MG content, the activities of SOD and CAT, accumulation of proline, GB, total phenols, Na^+ uptake in root and shoot, and total flavonoids were found to be increased. Overall, 24-EBL supplementation provided tolerance to soybean plants by upregulating the antioxidant system, AsA-GSH cycle, and glyoxalase system. Yusuf et al. [73] under completely randomized block design studied the BRs-mediated protection of growth and N metabolism and the potentiality of antioxidant system under Ni stress (0, 50, 100, or 150 mg/kg) in two cultivars of *Vigna radiata*, namely, PDM-139 and T-44. The role of two doses (10^{-8} or 10^{-6} M) of HBL in alleviating the Ni-induced damages via the ability of antioxidant enzymes and proline content was investigated. It was found that the Ni imposes toxic impact on the plants in a concentration dependent manner. The supply of HBL was effective in countering Ni stress as its application conferred tolerance up to 100 mg/kg in improving growth, nodulation, photosynthesis and yield attributes consequently. Fariduddin et al. [74] exposed *Cucumis sativus* L. plants to chilling stress to study the ameliorative role of HBL through studying the growth, photosynthesis, enzymes, and biochemical parameters. Cucumber seedlings were exposed to two chilling regimes, that is, 10/8 and 5/3°C for 18 h. The spray treatment consisted 10^{-8} or 10^{-6} M of HBL applied at 30-day stage to plants. Chilling stress imposes marked reductions in growth, chlorophyll, net photosynthesis, efficiency of photosystem II and alterations in NR and carbonic anhydrase (CA) activities. In contrast, the activities of antioxidant enzymes viz-CAT, POD, and SOD along with the proline content increased in response to chilling stress. HBL supply exerted a protective role via the maintained higher values of antioxidant enzymes and proline content under chilling stress. In order to assess the role of HBL (10^{-8} M) under two Cd doses (3 and 9 mg/kg sand) in *Solanum lycopersicum* plants, Singh and Prasad [75] designed an experiment in plant growth chamber. Treatment of plants to Cd stress resulted in a significant decrease in enzymes associate with N metabolism. The application of exogenous HBL supply ameliorated the ill effects of Cd stress by triggering an increase in growth, photosynthesis, protein and carbohydrate content and inorganic N and N assimilating enzymes. Kaur et al. [76] proposed the model of HBL-mediated regulation of antioxidant enzyme activities and gene expression in *Brassica juncea* plants to counteract the combined salt-and temperature-induced oxidative stress. HBL treatments (0, 10^{-6} , 10^{-9} , and 10^{-12} M) was applied as seed priming on plants exposed to the low (4°C) or high (44°C) temperature and salinity (180 mM) stresses. The combined treatments of salt and temperature significantly reduced length but increased H_2O_2 content and the activities of SOD, CAT, APX, GR, DHAR, and MDHAR. Application of HBL improved growth traits, reduced H_2O_2 and the response of plants was dose-dependent.

5. Role of ethylene

Phytohormone “ethylene” (ET) is a small gaseous plant growth regulator which is responsible for ripening of fruits and is known for inducing triple response in plants [77]. The growth-regulating effects of ET were first observed

by a Russian physiologist Dimitry K. Neljubov in 1901, however almost 60 years later in 1965 ET was established as a plant hormone [78]. Plant growth and senescence are chiefly regulated by the signaling mechanisms of ET [79–81]. However, it exerts its multifunctional role as one of the diversified signaling molecules to confer acclimatization to crop plants under various abiotic stresses. The signal perception of ET takes place at the membrane of endoplasmic reticulum and is bacterial two-component type which initiates a cascade signaling events through transcriptional regulation in the nucleus, thus eventually controlling a myriad of plant developmental events. Meanwhile, the interplay of ET with other signaling molecules provides adaptation to plants under various abiotic pressures [7, 8, 82–88]. Now, we will focus our attention on various reports on the functions of ET on tolerance toward major abiotic stresses in crop plants. Indian mustard plants were grown under 200 mg Zn/kg soil and the effects of 200 $\mu\text{L/L}$ spray of ethephon at 20 days after sowing (DAS) was tested to alleviate the Zn toxicity. The results after 30 DAS revealed that exposure to Zn stress causes toxicity by inhibiting photosynthesis and growth, while increasing the oxidative stress biomarkers. ET application (as ethephon) to Zn-stressed plants restored photosynthesis and growth of mustard plants by decreasing oxidative stress via augmenting antioxidant activity, the metabolism of proline, glyoxalase system, and optimum nutrient homeostasis [89]. In tomato plants, Alves et al. [90] provided new insights into the interactive role of ET on selenium-mediated antioxidant enzymes under Cd stress. Overall, the results suggested that cross talk of ET with Se manipulated the ET regulated expression of genes to induce Cd tolerance. The effect of Cr toxicity at 1.2 mM concentration given as $\text{K}_2\text{Cr}_2\text{O}_7$ after 10 DAS through nutrient solution on four cultivars of *Brassica juncea*, namely, Varuna, Pusa Bold, Rohini and SS2 were studied under ET supplementation [35]. Plants grown under Cr stress showed an enhanced accumulation of H_2O_2 , MDA content, and superoxide production and a marked reduction in photosynthesis and growth traits. Ethylene (2-chloroethyl phosphonic acid, 200 $\mu\text{L/L}$) boosted the activities of enzymes associated with S assimilation, proline accumulation, anti-oxidant defense system, ATP-sulfurylase and serine acetyl transferase, and GSH level and resulted in inhibition of stress ET levels to the optimal range under Cr stress, thus increasing the photosynthesis and growth. The key role of ET was further substantiated by using ET action inhibitor, silver nitrate (AgNO_3) in the reversal of Cr-induced changes. In *Brassica juncea* plants, alleviatory role of ET (200 $\mu\text{L/L}$ as ethephon) in the presence of 200 mg/kg soil each of Ni and Zn stress was investigated [91]. Application of ET reverses photosynthetic inhibition and promotes growth by inducing changes in PS II photochemistry, photosynthetic NUE, and modulation of antioxidant enzymes. The study got further confirmation by using ET action inhibitor-norbornadiene which reversed ET-induced changes. In *Arabidopsis thaliana*, Hartman et al. [92] studied the changes in NO and oxygen in controlling the stability of TFs in regulating of N-degron pathway and adaptation to flooding-induced hypoxia. They concluded that ET-mediated decrease in NO conferred tolerance to plants against hypoxia stress. The pretreatment of rice plants with the ET precursor under submergence stress plays a key role in the survival of rice plants [93]. ET signaling helped in the survival of rice seedlings under submergence stress by affecting intracellular redox homeostasis and antioxidant systems. Jegadeesan et al. [94] unraveled the proteomics involved in pollen of *Solanum lycopersicum* thermotolerance mechanisms mediated by ET. The quantitative analysis showed that heat stress-affected protein homeostasis and metabolism of carbohydrate and energy. ET (ethephon) increased pollen quality prior to heat stress exposure. According to gel LC-MS fractionation a total of 1355 proteins were identified. ET application shifted pollen proteome exposed to the heat stress closer to the proteome under non-stressful conditions and caused an upregulation into

the protective mechanisms against the heat-induced oxidative stress by causing a significant higher abundance of glutathione-disulfide reductase, glutaredoxin, and protein disulfide isomerase. Iqbal et al. [95] studied the potential of exogenously sourced ET (200 $\mu\text{L/L}$) under nutrient deficiency (40 mg N/kg soil) at 40 DAS. ET supply increased the stomatal conductance, photosynthesis, and promotes growth under low nutrient availability in mustard plants. Application ET also alleviated salt stress response in various crop plants. In fact, the alteration of ET signaling mechanism significantly affects the response of plants to salt stress [96]. Freitas et al. [97] worked out the capacity of ET in triggering salinity stress tolerance in maize plants. During NaCl exposure, a biphasic ET production (at 5.5 and 12.5 h) and decrease in total polyamine content was noticed in salt-sensitive plants. In the salt-tolerant genotype, there was lack of stress ET biosynthesis and this was attributed to the 1-aminocyclopropane-1-carboxylic acid oxidase (ACO) and *ZmACO5b* gene downregulation activity and expression. The ET was involved in promoting salt stress tolerance by activating pathways of signaling by H_2O_2 that is dependent upon enzymes of polyamine catabolism. Application of ET also improved the tolerance to salt tolerance in *Arabidopsis thaliana* by maintaining K^+ content in shoots and roots to an appreciable extent [98]. Gharbi et al. [99] showed that inhibition of ET biosynthesis minimizes salt (125 mM) tolerance in *Solanum chilense*. The involvement of ET was also ascertained in the alleviation of salt-induced photosynthesis and growth reductions in *Vigna radiata* L. [100]. A central role of ET in BRs-induced alternative respiratory pathway which played an important role in abiotic stress tolerance in *Cucumis sativus* L. has also been reported [88]. A critical role of ET for the maintenance of root growth and mineral homeostasis under excess Fe stress in *Arabidopsis thaliana* has also been reported [101].

6. Role of methyl jasmonate

Methyl jasmonate (MJ) is one of the conjugates of jasmonic acids (JAs) and are important as well as ubiquitous phytohormone distributed in plants [102]. MJ is implicated in plant responses to salt, drought, metal/s, and heat stresses. MJ exert its alleviatory role under abiotic stresses by modulating plant morphology and physiology to a great extent. Taheri et al. [103] studied the effects of exogenous MJ-mediated (0, 60, and 120 mM) improvements in physiological and biochemical traits of *Anchusa italic* plants under salinity (5, 10, and 15 dS m^{-1}). Salinity stress significantly decreased growth characters, RWC, chlorophyll a, total chlorophyll, soluble sugars, protein, and K^+ contents but at the same time induced a marked increase in proline, Na^+ , and Ca^{2+} contents. The application of MJ increases the aforementioned traits in plants grown under salt stress. In salt-tolerant rice genotypes, a higher concentration of MJ has been reported [104]. In wheat plants, application of 2.0 mM MJ ameliorated salt induced changes by boosting the expression of antioxidant enzymes, such as CAT, SOD and APX, and enhancing the GSH, chlorophyll b, and carotenoids contents [105]. In *Hordeum vulgare*, MJ-mediated (12 μM) regulation of genes of enzymes such as arginine decarboxylase, apoplastic invertase, and RuBisCo activase were found to be involved in imparting salt stress resistance [106]. The signaling of JAs promotes salt stress tolerance via the wheat allene oxide cyclase gene [107]. The wheat plants were exposed to saline stress conditions (12 dS m^{-1}) and the results showed that height of plant, leaf number per plant, tiller number, fresh and dry weight per plant, spike length, grain number per spike, grain weight per spike, and yield were reduced. MJ application mitigated the ill effects of salt stress by increasing the abovementioned traits in wheat plants [108]. In a polyethylene applied pot study, Tavallali and Karimi [109] studied the

effect of foliar application of MJ (0, 0.025, 0.050, and 0.075 mM) in enhancing salinity stress (0, 50, 100, and 150 mM) mitigation of almond root stocks. The MJ-mediated improvement in salt stress tolerance was attributed to the restriction of gene expression and activity of cytokinin oxidase which results in the inhibition of cytokinin decrease. MJ imparted salt tolerance by regulating the endogenous biosynthesis of phytohormones, expression of antioxidant activity, and gas-exchange traits of almond rootstocks. The possible role of MJ (0.25 mM) on the physiological responses and growth of *Fragaria × ananassa* cv. “camarosa” under salinity stress (0, 30, and, 60 mM NaCl) was investigated. Application of 0.25 mM MJ boosted the activities of antioxidant enzymes that ameliorated the salt-induced salinity stress effects [110]. Priming rice plants with MJ was reported to ameliorate the polyethylene glycol-induced osmotic stress [111]. In a recent study involving wheat plants, Allagulova et al. [112] applied MJ (0.1 μM) to unravel its alleviatory role under water-induced stress by investigating the potential participation of dehydrins. The stress was imposed by increasing the concentration of mannitol from 3 to 5% in the growth medium. Wheat seedlings pretreated with 0.1 μM MJ found to reduce the level of drought-induced retardations and enhanced the accumulation of the transcripts of *TADHN* dehydrin and proteins as well. In order to evaluate the effects of drought under exogenously applied MJ in wheat cultivars (Yu-Mai-1, Lu-Nong-116, HuaiMai-19, Yan-Nong-19, Bai-Maizi), a simple randomized complete design experiment was executed [113]. The drought was imposed at three stages: jointing, heading, or grain filling. The application of MJ was accomplished one week after the exposure of plants to the imposition of drought stress. The results showed that drought stress substantially decreased the growth and yield of all wheat cultivars reflected in the form of plant height, peduncle length, dry biomass of different plant parts, and also in yield. The application of MJ improved the drought resistance mainly by maintaining growth and yield traits of wheat plants. A pot-culture experiment in order to investigate the role of MJ presoaking (50 μM) for 8 h treatment on maize plants under water stress in the form of water field capacity (WFC) 65, 55, and 45% was setup. MJ application lead to an increase in plant height, fresh and dry weight, the pigment levels total carbohydrates, total soluble sugar, polysaccharides, free amino acids, proline, total protein, activities of CAT, POX and SOD and contents of N, P, and K and endogenous IAA but a decrease in ABA levels of wheat plants under stress condition [114]. In *Solanum lycopersicum*, the role of JA accumulation in the modification of water deficit-induced stomatal closure was studied. The drought stress-induced the closure of stomata that was correlated with the accumulation of JA, but in grafts of WT and *def-1* mutant which does not accumulate JA, the stomata was found to be insensitive [115]. Improvement of drought stress tolerance by the application of MJ has also been reported in soybean genotypes (Giza 22 and 35) [116], pear [117], sunflower seedlings [118], and *Cistus albidus* L. [119] plants. Nonetheless, application of MJ (10 μM) has been found to reduce chilling injury in cucumber by inhibiting the production of H₂O₂ [120]. MJ-mediated improvements in chilling stress tolerance in cold-stored lemon fruits has also been reported [121]. In case of metal/s stress, MJ application played a significant role in ameliorating the damages in physiology and morphology of diverse crop plants. The effect of exogenous MJ in two *Brassica napus* L. cultivars (ZS 758—a black seed type, and Zheda 622—a yellow seed type) was investigated against exposure to arsenic toxicity. MJ alleviates As-induced oxidative damages by significantly increasing chlorophyll fluorescence, biomass production and concomitant reduction in MDA and ROS contents. MJ application also maintained the high pools of GSH and AsA along with enhanced transcript expression SOD, APX, CAT, POD, and secondary metabolites (*PAL*, *PPO*, *CAD*) and reduction in As uptake [36]. Zaid and Mohammad [31] applied 1 μM MJ to test its alleviating capacity

against Cd (150 mg/kg) stress in *Mentha arvensis* plants. Cd applied through soil imposes restrictions in growth, physio-biochemical traits. The enhanced ROS accumulation and stomatal closure were also observed in plants grown under Cd stress. Application of MJ alleviated the Cd stress by reducing the damages in physio-biochemical traits along with reduced ROS detoxification. Pre-incubating *Phaseolus coccineus* plants with 10^{-5} M MJ has been found to minimize the Cu toxicity [122]. The identification of differentially expressed protein spots suggested the putative role of MJ in diverse physiological processes including oxidative tolerance and defense-related metabolism [123]. Thus, the above discussion clearly suggests that MJ alleviates the metal/s-induced oxidative stress by modulating the key physio-morphological traits in diverse crop plant to impart stress tolerance.

7. Conclusion and future outlook

Crop plants are exposed to myriads of abiotic stress conditions and undergo a significant retardation in growth and development, thus reducing crop productivity. Stresses are perceived, and modulation in the expression of genes encoding diverse proteins are induced in the signal transduction pathways in plants. Application of discussed phytohormones in the present chapter showed that the cross talk of phytohormones with various signaling agents under different stress conditions in diverse crop plants impart stress tolerance under stress pressures. A schematic representation on phytohormones-mediated abiotic stress tolerance is given in **Figure 1**.

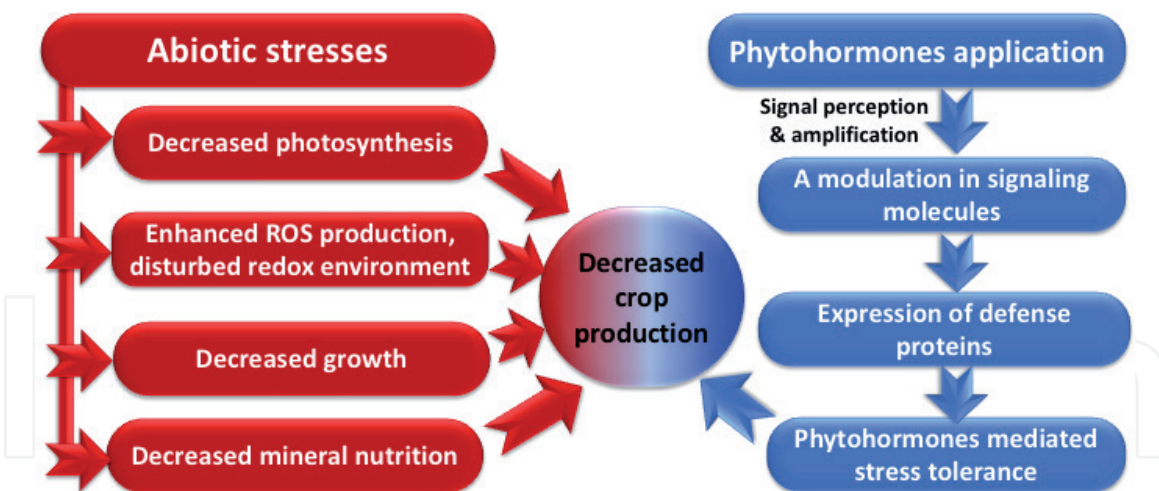


Figure 1.
Abiotic stress and phytohormones' signal transduction pathway in plants.

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