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Review

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Insights into Different Mitigation Approaches for Abiotic Stress in Horticultural Plants

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Highlights

- Abiotic stress considerably decreases the plant growth and development of horticultural plants.
- PGRs, PGPR and plant hormones significantly enhanced stress tolerance in horticultural plants.
- Integrated mitigation strategies protected leaf photosynthetic performance in plants.

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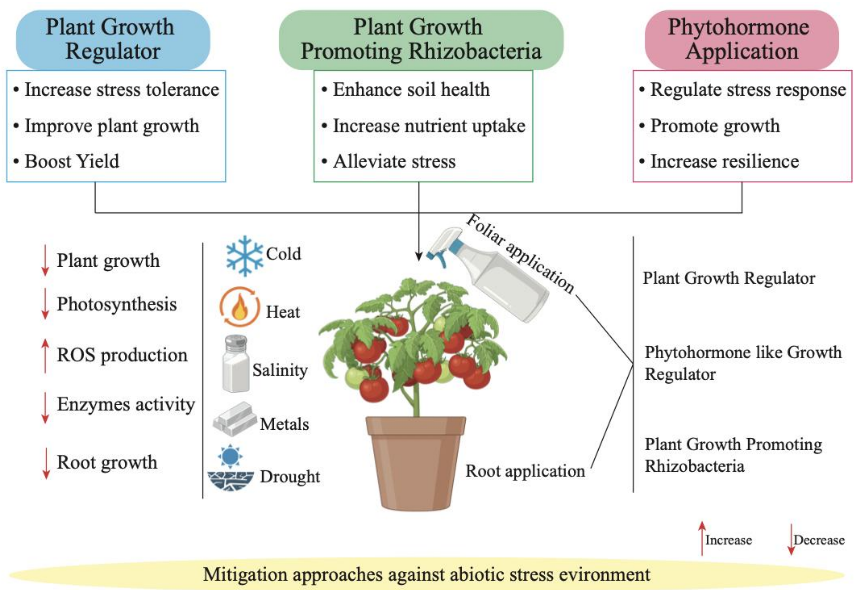
Graphical Abstract



Abstract

Horticultural crop yield has declined significantly due to climate change. Various abiotic stresses cause adverse effects on the productivity of horticultural crops. Abiotic stressors adversely affect germination, vegetative growth, reproductive phase, and the quality of produce in such plants. Plants modulate physiological and biochemical indices to mitigate the adverse effects of abiotic stressors. Recently, there has been a lot of interest in the integration of different stress mitigants to mitigate the adverse effects of abiotic stress on horticultural crops. Different stress mitigants have the potential to enhance the tolerance against abiotic stresses by promoting root growth, leaf transpiration, seed germination, and antioxidant levels while decreasing the overproduction of toxic reactive oxygen species. The current review explores the important roles played by various signaling molecules, plant growth regulators (PGRs), phytohormones, and plant growth-promoting rhizobacteria (PGPR) in horticulture plants to ameliorate abiotic stress tolerance. Therefore, the goal of this study is to provide an overview of the evolving ideas in abiotic stress tolerance, focusing on the productivity of horticultural crops. It also describes the various roles of different stress mitigants utilized in plants under stress conditions. This review highlights the potential of integrated stress-mitigation strategies as sustainable tools for improving the resilience and productivity of horticultural crops under changing climatic conditions.

Keywords: Cell metabolism, Membrane integrity, Oxidative damage, Phytohormones, Plant growth regulator

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1. Introduction

The production of horticultural crops is significantly hindered by climate unpredictability (Huang et al. 2024). Abiotic stresses are important factors that reduce crop yield globally (Klay et al. 2014). Abiotic stresses disturb the plant metabolism, and excess toxic substances, membrane rupturing, and ion leakage are causes that reduce plant growth and yield under such conditions (Wei et al. 2015). Innovations are required to bridge the gap between food supplies worldwide and demand because traditional approaches are ineffective in addressing the intricate traits linked to stress resilience. Innovative and efficient techniques must be developed to address these concerns (Misra et al. 2014). To fulfill the growing global demand for food, significant changes are needed. Thus, it is imperative to develop excellent practical approaches that improve plant growth and yield under stressed conditions. Some practical approaches, such as signaling molecules, phytohormones, plant growth-promoting rhizobacteria (PGPR), soil microbes, nanotechnology, and molecular alterations can be used for the characterization and evaluation of tolerant germplasm (Muhammad et al. 2024a).

Signaling molecules are widely used because they effectively prepare plants to withstand abiotic stress challenges despite requiring significant energy utilization on defense-related systems (Akram et al. 2021). Plants treated with signaling molecules such as melatonin (MEL), dopamine, gamma-aminobutyric acid (GABA), nitric oxide (NO), and serotonin have excellent potential to activate the defense mechanism against abiotic stresses (Ansari et al. 2021). Activation of antioxidants results in the scavenging of toxic substances such as ROS that are overproduced due to adverse conditions of abiotic stress (Yuan et al. 2023). Abiotic stress resilience is thought to be primarily accomplished through abscisic acid (ABA) and salicylic acid (SA) induced signaling channels, while GABA-induced defense for biotic stresses is primarily achieved by jasmonic acid-dependent governed defense systems (Ansari et al. 2021). Therefore, signaling molecules contribute to the activation of defense system of plants under stress situations.

Phytohormones are effective for the improvement of abiotic stress tolerance. The application of phytohormones is an effective way of cultivating climate-resilient plants for higher yield (Bajguz and Hayat, 2009). Phytohormones are an environmentally acceptable way of enhancing abiotic stress resilience in plants, especially in case of horticultural crops (Muhammad et al. 2024b). According to Saini et al. (2021), phytohormones are chemical mediators secreted by plants that regulate how plants respond, grow, and mature in response to environmental stressors. According to Podlešáková et al. (2019), phytohormones play a crucial role in abiotic stress tolerance by regulating diverse signaling pathways. Furthermore, they participate in the oversight of various exogenous and endogenous stimuli, which leads to significant modifications in the growth of plants (Muhammad et al. 2023). Limited research on horticultural plants has been carried out to elucidate the beneficial roles of phytohormones in abiotic stress tolerance (Podlešáková et al. 2019; Muhammad et al. 2024a).

Huge crop production losses occur due to abiotic stresses each year. Earlier research has shown that PGPR have a huge potential to help crops cope with a wide range of abiotic stresses (Kumar et al. 2019). Tolerance to abiotic stresses and increased crop production and growth have been noticed among several plants through PGPR treatment (Dimkpa et al. 2009). PGPR helps plants tolerate abiotic stresses by using different ways, such as regulating the production of phytohormones, inducing stress-responsive genes, the production of volatile organic carbon compounds, producing osmolytes to regulate osmotic balance, producing exopolysaccharides, enhancing soil physical properties, and producing phytohormones (Paul et al. 2017; Shameer and Prasad, 2018). A possible method for boosting crop yields in adverse conditions is the assessment, selection, and inoculation of PGPR that are resilient to abiotic stresses as antibiotics.

Appropriate management practices are employed by plant researchers to boost output under abiotic stresses. An efficient potential strategy for addressing the negative effects of abiotic stresses on crop sustainability is the phytohormone spray (Ali et al. 2023). Plant researchers are paying close attention to stress mitigants because of their multifunctional contribution to abiotic stress mitigation (Javid et al. 2011; Ahmad et al. 2023). However, their application in horticultural crops subjected to abiotic stress tolerance still needs to be fully uncovered. Exploring the functions of different stress mitigants in various plant processes, particularly physiological and biochemical aspects, has been widely addressed in recent research on abiotic stress resilience. The main goal of the current review is to examine the beneficial roles of signaling molecules, phytohormones, and PGPR in horticultural plants through the modulation of morphological, physiological, and biochemical indices.

2. Signaling Molecules Contribution in Mitigation of Adverse Effects of Abiotic Stress

2.1. Serotonin

Serotonin is a naturally occurring indoleamine as well as an extremely potent antioxidant (Erland et al. 2019). Serotonin is known to regulate plant development and is a hormone-signaling molecule that regulates stress response in plants. Serotonin can increase root formation, the number of shoots, and the number of leaves. Serotonin can promote germination, raise coleoptile weight, total biomass output, and hypocotyl elongation during germination. Furthermore, serotonin may be the principal messenger in plants and a major regulator of phytochrome action (Mukherjee, 2018). Serotonin level has been shown to change during the ripening of banana (Roshchina and Yashin, 2014). It also promotes the sprouting of seeds in radish seedlings. Additionally, serotonin has a significant role in environmental stress. Serotonin might have the potential to boost salinity tolerance because of its capacity to regulate ion influx through chloroplasts (Roshchina, 1990). Hence, serotonin supplementation can be effective in the survival of plants under heavy metal metal stress.

2.2. Gamma-aminobutyric Acid

GABA is a widely known signaling molecule that plays several functions in plants. Malekzadeh et al. (2014) reported that GABA causes a significant decrease in MDA levels and an improvement in the antioxidant balance in tomatoes during cold-related stress. GABA is the main mediator of senescence of leaves brought on by oxidative damage. Thus, by enhancing the photochemical capacity and turning on the antioxidant defense system in response to light stress, GABA enhances tolerance in pepper against light stress (Li et al. 2017). Pretreating peach fruits with GABA prevented chilling harm, enhanced the activity of antioxidant enzymes, and maintained their nutrient levels (Podlešáková et al. 2019). By postponing plant aging, GABA enhances endurance to abiotic stressors and is crucial for stress adaptation (Khan et al. 2021). The stress-responsive signaling molecules, like GABA, protect plants from oxidative damage by lowering ROS accumulation in strawberry (Golnari et al. 2021). Plant resilience to abiotic stress is being successfully increased by the use of GABA priming. By reducing the distribution of stress-related metabolites and raising defense-related metabolites, GABA (2 mM) promoted black pepper defense during polyethylene glycol (PEG- 10 % w/v) induced stress, revealing osmotic stress resilience (Vijayakumari and Puthur, 2016). Under calcium nitrate stress, GABA supplementation enhances the growth, yield, and overall quality of muskmelon. GABA treatment significantly enhanced peach biomass production, levels of chlorophyll, as well as antioxidant enzymes during cold stress, while also reducing the generation of ROS and maintaining the integrity of the cell membranes (Shang et al. 2011). The main modulator of oxidative stress-induced leaf senescence is GABA. GABA boosts the stress resilience of chilies during light extremities by boosting their photochemical capacity and activating the antioxidant defense system. Li et al. (2017) found that the application of GABA resulted in a boost in the exchange of gaseous attributes, chlorophyll pigments, fluorescence features, as well as a reduction in MDA levels in chilies. GABA exposure effectively raised the amount of polyamine biosynthesis while lowering putrescine as well as spermidine content of leaves (Hu et al. 2015). GABA dramatically enhances morpho-physiological characteristics of plants under abiotic stress, including photosynthesis, soluble sugar, as well as proline synthesis, and polyamine breakdown (Golnari et al. 2021). GABA reduces the generation of ROS resulting from stressful conditions through the activation of ROS scavengers. GABA has the potential to reduce ion leakage through the membranes by balancing the electron transport chain within plant cells (Shang et al. 2011). GABA supplementation has the potential to regulate signaling molecules and the expression of stress-related genes (Podlešáková et al. 2019).

2.3. Nitric Oxide

A crucial signaling molecule, NO, plays a role in several plant activities, including blooming, fruiting, stomatal regulation, biosynthesis, seed dormancy, seed growth, and development (Hawrylak-Nowak, 2009). By enhancing the activity of antioxidant enzymes, sodium nitroprusside (SNP), a NO source, reduced the adverse impacts of ROS on plant growth. Numerous crops, including cucumber (Shi et al. 2007), spinach (Du et al. 2015), and pakchoi (Ren et al. 2020), have also been shown to benefit from NO spraying, which helps enhance the capability of plants to tolerate salinity stress. Additionally, it is useful in strengthening mechanisms for tolerance in higher-growing plants that are cultivated in arid climates (Manai et al. 2014).

By controlling the amount of ROS as well as endogenous hormones, by causing transcriptional modifications of genes engaged in various functions like signaling, defense, cellular death, delivery, fundamental metabolic processes, and ROS generation, NO contributes an essential part in cryoprotection (Lamattina et al. 2003). Although NO has antioxidant effects to mediate cell redox balance that regulates the inhibition of oxidation-related harm in plants. It also promotes the conversion of O_2^{-} to H_2O_2 and increases the H_2O_2 scavenging events (Lamattina et al. 2003). Hence, NO is a crucial signaling molecule that plays an array of physiological activities in plants.

NO combines with ROS, hemes, proteins, and thiols to generate biological signals that either directly or indirectly control enzyme activity (Pagnussat et al. 2002). The placement and level of NO determine its effects. According to Leshem and Haramaty, (1996), supportive reactions mitigate the effects of oxidative as well as nitrosative stressors, but harmful reactions result in cell death as well as reactive and nitrosative harm when NO levels are high. NO aids in the adaptability of structures and functions, as well as the acclimation of trees. A novel experimental strategy and preventative strategies to manage stress signals across conifer life histories are provided by the application of NO donors and inhibiting enzymes (Neill et al. 2003).

2.4. Melatonin

MEL is a naturally occurring, powerful antioxidant molecule that is being extensively studied for its potential to reduce stress as well as boost antioxidant levels (Huang et al. 2022). MEL (150 µM) effectively reduces the negative effects of salinity stress by boosting the photosynthetic mechanism, defensive photosystem process, and upregulating antioxidant enzyme system as well as their gene expression in bitter melon (Sheikhalipour et al. 2022). MEL also improves salinity resilience as well as reduces oxidative injury in cucumber (Zhang et al. 2020). Furthermore, MEL boosts the activities of the H^+-pump, which leads to elevated K^+ influx and Na^+ efflux, which maintains K^+/Na^+ homeostasis as well as reduces Na^+ toxicity. MEL improves salt stress resilience in pea (Yusuf et al. 2024), broccoli (Sardar et al. 2023), and okra (Zhan et al. 2021). MEL has the potential to reduce electrolyte leakage; however, antioxidant enzyme activity and chlorophyll pigments were enhanced under salinity stress in rosemary plants as studied by Mohamadi and Karimi, (2020).

Fresh water sources must always be available for agricultural output to function, and as these resources become scarcer, drought-related stress is one of the biggest issues for farming purposes (Parkash and Singh, 2020). Applying MEL spray may be a suitable method for improving the productivity of cauliflower cultivated in drought-stressed environments (EL-Bauome et al. 2022). Improved photosynthesis, which lessens MDA in chrysanthemum plants and mitigates drought-induced oxidative stress, is responsible for the improved tolerance brought about by MEL spray (Luo et al. 2023). Supplementing with MEL enhances the growth by boosting the function of antioxidants in fenugreek (Zamani et al. 2020). Drought stress results in poor growth, low yield, disturbance in plant vigor, damage to Photosystem II (PSII) reaction centers, rupturing of cell membranes, and overproduction of toxic substances in tomato plants. Therefore, supplementation of MEL boosts the antioxidant level, regulates signaling molecules, and activates the defense system of tomato under drought conditions (Liu et al. 2015). According to Zhao et al. (2016), MEL improved the chloroplast cell ability to tolerate cold in cucumber seedlings by improving ascorbates, which improves the potential for ROS elimination, and by maintaining the photosynthesis electron flux transportation, which reduces ROS generation. Through the regulation of genes governing the chilling stress response of mustard, MEL improved the ROS detoxification ability and elevated the amounts of osmotic modifying compounds to assist in preserving osmotic cellular capacity during chilling stress (Muhammad et al. 2024b). In eggplants, MEL reduced the negative effects of chilling stress (Yakuboglu et al. 2022). Potato tuber yields improved due to supplementation of MEL against cold stress (Golovatskaya et al. 2024).

Exogenous MEL increased the adaptability level toward heat stress in tomatoes (Jahan et al. 2021a) and chrysanthemums (Xing et al. 2021). In addition to improving the oxidase activity and chlorophyll levels and lowering the degree of heat damage to celery seedlings, it also increased leaf transpiration as well as the efficiency of the photosynthetic apparatus (Li et al. 2022). When cherry radish was subjected to heat stress, MEL significantly increased the biomass output and antioxidant activity of enzymes (Jia et al. 2020). In tomatoes subjected to heat stress, MEL significantly protected the photosynthetic framework, the utilization of carbohydrates, and the elevation of photosynthetic parameters (Jahan et al. 2021b). When tomatoes were subjected to heat stress, MEL increased the development and activity of antioxidant enzymes (Jahan et al. 2021b). MEL reduced the buildup of ROS in tomato departs under chromium distress (Sun et al. 2023); raised photosynthesis in peppers against chromium distress (Rizwan et al. 2024); boosted pigment content in spinach under boron distress (Moussa and Algamal, 2017); boosted antioxidant enzyme production in tomato plants under aluminum stress (Ghorbani et al. 2023); controlled cucumber performance against copper stress (Cao et al. 2019); and boosted mineral retention in tomato seedlings under nickel pollution (Jahan et al. 2020). Moreover, Jahan et al. (2020) also found that MEL supplementation decreased the accumulation of nickel in tomato seedlings. The contribution of signaling molecules in horticultural crops is imperative to explore for sustainable crop production (Table 1).

MEL supplementation boosted pea growth and development under harmful arsenic conditions. Furthermore, MEL treatment decreased oxidative harm by reducing the ROS accumulation in pea leaves (Ahmad et al. 2023). MEL improved the overall performance of radish plants under Cd stress (Xu et al. 2020). After applying MEL to cucumber plants under either high or low iron stress, the physicochemical aspects that included a higher concentration of endogenous MEL, as well as a decrease in buildup of ROS were regulated (Ahammed et al. 2020). Deep insights into the biological, physiological, and genetic foundations have also been studied to combat the negative effects of abiotic stresses (Fig. 1).

3. Plant Growth Regulator Potential in Alleviation of Abiotic Stress Tolerance in Plants

3.1. Auxins

Auxin is an important phytohormone necessary for proper plant growth and development. Moreover, it has an excellent contribution in plants against abiotic stress tolerance (Zhang et al. 2020). Pre-sowing auxin treatment to seedlings amplifies the growth-limiting effect of osmotic damage, as documented by earlier findings of Olaiya, (2010). Similarly, Vidoz et al. (2010) investigated that auxin buildup leads to ethylene production, which in turn builds adventitious roots toward the bottom of the stem. Comparably, Muday et al. (2012) proved that adventitious root formation is facilitated by the cross-interaction of ethylene as well as natural auxins in plants. Molecular research aimed at better understanding the auxin function has revealed that certain auxin-sensitive genes are also capable of responding to drought-related stress. Plants resistant to drought are better able to withstand stress when genes involved in auxin synthesis and polar transport are overexpressed. Therefore, it has been investigated that auxin can help plants to overcome challenges brought on by abiotic stress. Ostrowski et al. (2016) studied that auxin component indole-3-acetic acid–aspartic acid (IAA-Asp) affects the pea crop under Cd by altering the way enzyme's function, as well as by reducing ROS levels and stimulating protein carbonylation. Auxin is also widely recognized for its critical role in improving the root growth of plants growing under stress and normal conditions (Saini et al. 2021).

Dunlop and Binzel, (1996) observed the reduction of auxin concentrations under salinity stress in tomato plants. Auxin application improved fruit formation, resulting in a significantly higher yield of tomato plants (Ramin, 2003). Auxin treatment dramatically decreases

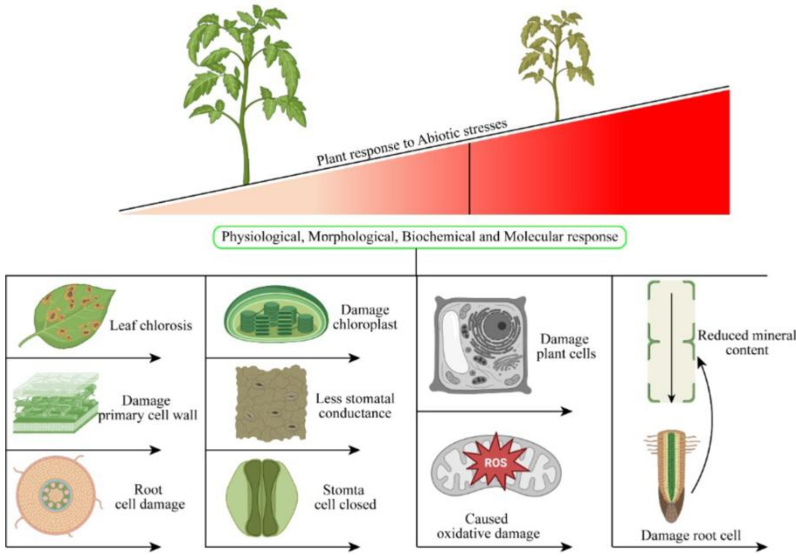

Fig. 1. Morpho-physiological and biochemical responses of plants under abiotic stresses.

Table 1. The beneficial role of signaling molecules in the amelioration of abiotic stress tolerance in horticulture crops.

Signaling molecules	Stress type	Species	Findings	Reference
GABA	Nitrate	Muskmelon	Promoted polyamine production, enhanced enzyme activity, reduced putrescine accumulation in leaf	Hu et al. (2015)
MEL	Iron	Cucumber	Enhanced biomass production, increased antioxidant enzyme activity, reduced excessive iron uptake	Ahammed et al. (2020)
Dopamine	Cold	Watermelon	Promoted proline accumulation, enhanced antioxidant enzyme activity, reduced oxidative damage	Jiao et al. (2021)
GABA	Low light	Pepper	Protected photosynthetic system, enhanced antioxidant enzyme activity, reduced ROS uptake	Li et al. (2017)
MEL	Drought	Pea	Upregulated antioxidant enzyme activity, protected photosynthetic apparatus, increased biomass yield	Ahmad et al. (2023)
MEL	Aluminum	Tomato	Restored growth parameters, promoted seedling growth, reduced oxidative damage	Ghorbani et al. (2023)
NO	Salinity	Pakchoi	Promoted seedling growth, improved seed germination, and reduced oxidative damage	Ren et al. (2020)
NO	Salinity	Cucumber	Reduced lipid peroxidation, MDA level, increased antioxidant defense system, and chlorophyll content	Shi et al. (2007)

MEL = Melatonin, GABA = gamma-aminobutyric acid; NO, nitric oxide; ROS = reactive oxygen species; MDA = malondeldehyde

ROS generation and improved photosynthetic enzyme function in cucumbers during cold stress, according to a recent study by Zhang et al. (2020). It significantly increased auxin efflux transporters as well as auxin biosynthesis transcription in plants under conditions of Cd exposure (Asgher et al. 2015).

3.2. Gibberellins

Gibberellins are naturally occurring plant growth hormones in plants (Castro-Camba et al. 2022). Their contribution is effective for sex expression, proper growth, and the yield of plants. Gibberellic acid (GA) of about 10 µM concentration enhanced seed germination and improved seedling growth of pea plants under chromium toxicity (Gangwar et al. 2011). Moreover, exposure to GA also changed the functioning of enzymes that regulate the processes of ROS removal and nitrogen production in pea plants (Gangwar et al. 2011). When barley is treated with GA, the adverse impacts of Cd as well as molybdenum on important plant functions, such as seed germination, were lessened (Siddiqui et al. 2020). Plants under challenging circumstances require gibberellin homeostasis for their sufficient growth (Castro-Camba et al. 2022). Hormonal growth retardants are used to control crop growth and have been shown to encourage drought tolerance. A great deal of the knowledge regarding the role of investigated hormones in adaptability to stress comes from these studies (Rademacher, 2000). These substances primarily affect plants by blocking the synthesis of gibberellin to promote healthy development, as well as adequate moisture levels. Siddiqui et al. (2020) showed that gibberellins (GA_3) use increased the assimilation of nutrients, number of leaves and branches, and yield of horticultural crops during drought conditions. Additional investigation suggests that GA_3 plays a part in reducing the growth inhibition in plants caused by NaCl. In addition to altering the ion balances in plants, GA_3 increases the absorption of numerous minerals while decreasing the uptake of Na^+. Through triggering enzymes that participate in the synthesis of RNA and proteins, exogenously administered GA_3 lowers drought stress (Siddiqui et al. 2020). In celery, the crosstalk between drought and GA3 is essential for bolting, cellular breakdown, and petiole elongation. Even in situations of a severe water deficit, GA_3 treatment in tomatoes has been demonstrated to reduce stomatal integrity and increase plant water requirements. Comparably in fruit crops that are experiencing drought, GA3-priming increases fruit set and size (Siddiqui et al. 2020). In drought conditions, seed germination is improved by GA_3 treatment. Interactions in cross-reactivity between various phytohormones provide one possible route. So, auxin is probably going to boost GA production. Similarly, the treatment of GA enhances the production of ABA (Gonai et al. 2004).

Table 2. Contribution of different plant growth regulators to cope with the adverse effects of abiotic stresses in horticulture crops.

Species	Stress type	PGR	Findings	Reference
Lettuce	Chemical	Gibberellins	Reduced ABA content, increased ABA catabolism, and improved seed germination rate	Gonai et al. (2004)
Grape	UV-B	ABA	Increased photosynthetic pigment content, phenolic content, and antioxidant enzyme activity	Berli et al. (2010)
Cucumber	Cold, heat	Ethylene	Increased enzyme activity, reduced oxidative damage, and improved AOX activity	Wei et al. (2015)
Tomato	Temperature	Auxin	Increased temperature stress tolerance by increasing the number of flowers and yield-related traits	Ramin, (2003)
Pea	Chromium	Gibberellins	Increased enzyme activity, nitrogen metabolism, and chromium stress tolerance	Gangwar et al. (2011)
Cucumber	Chilling	Auxin	Decreased EL level, MDA concentration, increased enzyme activity, and photosynthetic capacity	Zhang et al. (2020)
Tomato	Heat	Ethylene	Increased heat stress tolerance by regulating heat-related responsive genes	Pan et al. (2019)
Tomato	Cobalt	ABA	Reduced excessive ROS uptake and decreased metal uptake in leaves, and increased antioxidant system	Kamran et al. (2021)
Cucumber	Salt	BRs	Enhanced salinity stress tolerance, enzyme activity, seed germination, and reduced oxidative damage	Wang et al. (2011)

ABA = abscisic acid; AOX = alternative oxidase; ROS = reactive oxygen species; EL = electrolyte leakage; MDA = malondialdehyde.

Different plant growth regulators have excellent potential to mitigate the adverse effects of abiotic stresses (Table 2).

3.3. Abscisic Acid

Plants' capability to tolerate abiotic stress is significantly reduced by abscisic acid impairment. One major osmotic problem that hinders plant growth and causes large losses in horticulture farming is water-deficient conditions. Several physiological activities, such as photosynthesis, as well as moisture status, are hindered by stomatal conductance (Javid et al. 2011). More water is lost through the leaves than is taken from the roots, so plants may suffer damage (Robertson et al. 1987). ABA builds up in the gaps between cells that surround the stomata, which results in stomatal conductance as well as conserving water under drought stress. Numerous metabolic as well as morphology functions, as well as developmental stages, i.e., plant growth, dormancy of seeds, seedling emergence, embryo morphogenesis, stomatal closure, and the synthesis of lipids as well as storage proteins during abiotic stress, are all regulated by ABA (Salvi et al. 2021). Numerous horticultural crops, which have been subjected to abiotic stress, were found to exhibit boosted endogenous ABA phases, including cucumber (Wang et al. 2011), grapes (Berli et al. 2010), and petunia (Estrada-Melo et al. 2015). These findings indicate that ABA is essential in mitigating the adverse effects of abiotic stress. Furthermore, pretreating pepper seedlings with ABA decreased ROS during chilling stress. ABA treatment increased the activation of genes and decreased Zn assimilation and buildup in grapes (Song et al. 2019). Recently, it has been reported that ABA treatment enhances tomato biomass output, chlorophyll content, and root shape while also preventing cobalt uptake. Additionally, oxidative stress indicators decreased while antioxidant enzyme activity rose in tomatoes (Kamran et al. 2021). Different phytohormones had the potential to alleviate abiotic stress tolerance in plants (Fig. 2).

3.4. Ethylene

Ethylene promotess flowering, petal breakdown, fruit ripening, germination of seeds, growth of roots, and leaf withering (Groen and Whiteman, 2014). Plant growth as well as lifespan are primarily controlled by ethylene signaling mechanisms. *LeCBF1* expression in tomatoes was discovered to be influenced by exogenous ethylene and 1-methylcyclopropene (1-MCP), and it was not synthesized without freezing initiation (Zhao et al. 2009). The use of ethylene considerably reduced cell death and increased shoot as well as root growth (Klay et al. 2014). Additionally, the tomato gene *Sl-ERF.B.3* responds to abiotic stress. Abiotic stressors like salinity and cold temperature can change the endogenous ethylene concentrations in horticultural plants. Tolerance is enhanced with increasing ethylene levels. In horticultural crops such as sweet potato (Chen et al. 2013), tomato (Pan et al. 2019), and pepper (Siddikee et al. 2011). Ethylene boosts plant defense systems in response to environmental hazards. Moreover, ethylene controls the production of adventitious roots and primary roots in various plant species (Qin et al. 2019). However, Khan et al. (2020) claimed that ethylene plays a critical role in controlling signaling, metabolic processes, and plant growth concerning nutritional adaptation. During extreme salt stress, ethylene treatment dramatically improved the growth characteristics, gas exchange components, and photosynthesis of tomato. The ethylene significantly contributed to the resilience to abiotic stress of cucumbers by being a key player in the brassinosteroids-induced alternative metabolic route (Wei et al. 2015). Hence, ethylene treatment is crucial in helping horticultural plants cope with an array of abiotic stressors.

4. Phytohormone Enhances Stress Tolerance in Horticultural Crops

4.1. Brassinosteroids

A class of naturally occurring plant steroids known as brassinosteroids (BRs) is essential for abiotic stress resilience (Bajguz and Hayat, 2009). Treatment with BRs may boost ABA levels and mitigate the detrimental effects of drought (Kaya et al. 2020). The adaptability of eggplants to saline conditions is demonstrated by the lowered levels of Na^{+} as well as Cl^{-}, increased levels of K^{+} and Ca_2^{+}, and raised antioxidant enzyme activity. Cucumber plants grown in saline environments have lower amounts of nitrates and ammonium upon 24-Epibrassinolide (EBR) treatment. Nonetheless, foliar application of EBR to rapeseed at 30 as well as 45 days post-sowing may effectively alleviate the adverse consequences of salt stress (Zhang et al. 2022). The enhanced BR-induced resilience of cucumber under salinity is associated with higher levels of photosynthesis, nitrogen efficiency, as well as polyamines (Wei et al. 2015). The regulation of DNA methylation, which is essential for coping with salt, has recently been associated with BRs. The observation that priming seeds with EBR increases overall methylation as well as improves adaptation to salt indicates a potential involvement of BRs in epigenetic modification during salinity stress (Wang et al. 2011). BRs manipulations can mitigate the long-term impacts of drought on crops (Nawaz et al. 2017). After a week-long dearth of water, mustard plants continue to exhibit inadequate development as well as photosynthesis even after 60 days. However, supplementation of 24-epibrassinolide improved growth. BRs supplementation decreases ROS generation under drought stress (Khamsuk et al. 2018). Exogenous application of BRs increases tolerance to an array of abiotic stressors, including drought. Mutants that are BR-deficient and BR-insensitive have simultaneously shown enhanced resilience to stress. The endogenous BRs improve resilience to drought stress in tomato. However, *BRI1* upregulation had a detrimental effect on tomato resilience to drought, suggesting that anomalies in the BRs pathway could increase or decrease resilience to stress and highlighting the intricate relationships between BRs and stressors (Lv et al. 2020). BRs manipulations can mitigate the long-term impacts of drought on crops (Nawaz et al. 2017). Extreme temperatures reduce net photosynthesis and interfere with photochemical reaction processes connected to photosystem II (Li et al. 2015). EBR (0.2 mM) treatments can lessen photosynthetic deficits in tomato caused by extreme temperatures by improving the activities of antioxidant enzymes that lessen oxidative harm during stress. The finding that BRs can enhance thermo-tolerance in crop genotypes which are both heat-sensitive as well as heat-tolerant is important (Zhang et al. 2013). The photosynthesis pigment, total CO_2 assimilation level, closure of stomatal pores, photo-degradation function of PSII, as well as water utilization rate of melon that are heat-tolerant as well as heat-sensitive are all markedly increased by EBR.

Using bioactive compounds and modifying endogenous hormones and signaling processes, stress caused by heavy metals can be lessened by using phytohormones. Many plant species can benefit from BRs by lessening the impact of heavy metal stress (Singh et al. 2016). Photosynthesis was significantly decreased after 40 days of Cd stress in tomato plants (Ahammed et al. 2013). Under Cd stress, foliar EBR (0.1 mM) treatment significantly regulates photosynthesis (Vardhini, 2016). According to Yang et al. (2019), EBR may mitigate the chromium effects on the growth, oxidative ability, and PSII redox responses of cucumber. Tomato plants treated with EBR (0.1 mM) are more able to withstand Cd stress. Similarly, foliar spraying of BRs can improve chilling stress tolerance and activate the antioxidant defense mechanism in peach fruit (Yang et al. 2011).

4.2. Salicylic Acid

Salicylic acid (SA) enhanced the potassium content and decreased the uptake of Na^+ in garlic crops under salinity stress. The flower size of calendula plants was significantly decreased under salinity stress. However, morpho-physiological characteristics under salt exposure were noticeably enhanced by SA (2 mM) treatment in calendula (Bayat et al. 2012). SA-treated tomato plants grew more effectively when exposed to salt stress. Under salinity, leaf photosynthesis was restored by SA supplementation (Mimouni et al. 2016). Treatment with salinity boosted ROS, unbalanced mineral build-up, and inhibited spinach development (Nigam et al. 2022). SA controls tomato growth in stressful conditions (Naeem et al. 2020). In strawberries grown under salt stress, SA significantly decreased the uptake of salt and raised the uptake of potassium, proline levels, and activity of antioxidant enzymes (Roshdy et al. 2021). Drought-related damage was greatly reduced by SA in tomato (Fan et al. 2022). Comparably, applying SA improved the photosynthesis as well as the development of cucumber (Baninasab, 2010), eggplant (Wakchaure et al. 2020), watermelon (Silva et al. 2023), and pepper (Kaya, 2021). SA decreased oxidative harm by lowering the MDA level in strawberries under extreme drought (Sun et al. 2013). SA significantly decreased fatty acid levels and improved drought tolerance in pumpkin, according to Biareh et al. (2022). The use of SA controls roots architectural system and enhances the photosynthetic mechanism in olive trees (Brito et al. 2018). SA decreased the uptake and translocation of Cd in the shoots (Popova et al. 2009). Additionally, Gupta and Seth, (2021) found that tomato seedling growth was obstructed by the Cr toxicity. On the other hand, tomato seedling development is positively regulated by SA supplementation. When tomato seedlings were exposed to Cr toxicity, SA decreased Cr buildup and enhanced leaf exchange of gas properties. In potato leaves exposed to Cd toxicity, SA treatment dramatically lowered ROS and Cd transportation across roots to shoots. SA applied topically to potatoes boosted the amount of antioxidant enzymes (Li et al., 2019). In two peanut genotypes exposed to Cd stress, SA increased the antioxidant enzyme activity against Cd stress (Xu et al., 2015). SA controls bell pepper growth and increases the concentration of fatty acids under cold stress (Ge et al. 2020). SA dramatically reduced electrolyte leakage and lessened oxidative injury in spinach during cold stress, demonstrating a significant improvement in cold-stress endurance. SA treatment boosted the activity of antioxidant enzymes in spinach (Shin et al. 2018). Foliar treatment greatly enhanced the growth properties of spinach leaves (Min et al. 2018). After being treated with SA, eggplant seedlings exhibited a notable enhancement in antioxidant enzyme function, along with an upregulation in gene expression concentrations. SA significantly reduced oxidative damage in eggplant leaves under cold stress (Chen et al. 2011).

Through preventing cellular membrane harm in tomato seedlings during extreme temperatures, SA preserved the photosynthetic machinery, regulated the antioxidants, lessened ROS, restored pigment concentration, and decreased oxidative damage (Jahan et al. 2019). According to Khan et al. (2014), SA effectively enhanced root traits and root functionality in tomato plants subjected to heat stress. Heat stress was mitigated through the supplementation of SA in melon plants (Widiastuti et al. 2013). Exogenous spray of SA

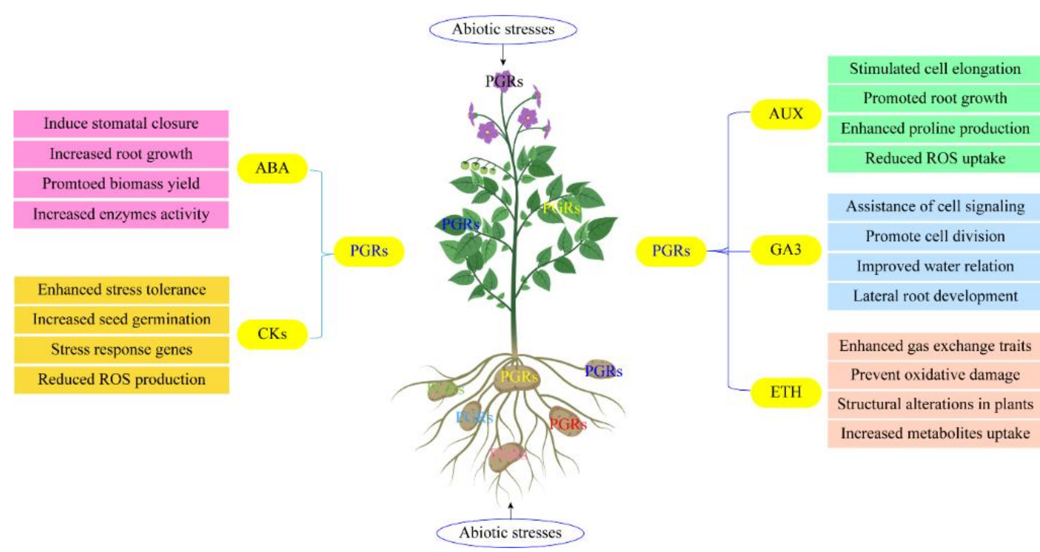

Fig. 2. Different phytohormones had the potential to alleviate abiotic stress tolerance in plants. ABA = abscisic acid, PGRs = plant growth regulators, CKs =

cytokinins, AUX = auxins, GA3 = auxins, ETH = ethylene

improved heat stress resilience and boosted the activity of antioxidant enzymes in young grape plants (Wang and Li, 2006).

4.3. Jasmonates

Jasmonates are imperative phytohormones contributing to the regulation of physiological and biochemical indices of plants growing under abiotic stresses to attain higher yield (Moradmand et al. 2015). Pigmentation reduction and tuber growth can be managed using jasmonates. The hormonal application to the foliage increased sugar beetroot output and improved its resistance to abiotic stressors (Koda, 1992). Although jasmonates were applied exogenously, their natural production was boosted, making them useful for hormone regulation. Methyl jasmonates improved reactive bioactive compounds, increasing drought resistance in cauliflower. Consequently, jasmonate spray has been shown to increase crop output (Meyer et al. 1984). Jasmonates serve as a protective mechanism in horticulture crops against environmental stresses. Horticultural crops that endure cultivation in harsh, saline conditions benefit greatly from these. It is possible to reduce environmental dangers by using jasmonates (Raza et al. 2021). Jasmonates possess a great deal to offer as a defense system for crops in agriculture in climate-related parts (Ruan et al. 2019). The role of each endogenous hormone as well as intrinsic jasmonic acid and its components, is important in defense mechanisms in melon under abiotic stressors (Xing et al. 2020). Phytohormones can be identified in cells of plants in various amounts, and studies often link these differences to modifications in the regulation of specific genes affected in their production and the processes that they govern in both stress and normal conditions. When crops were undergoing cold stress, foliar spraying jasmonic acid enhanced their resistance to salt stress (Moradmand et al. 2015). After being treated with jasmonic acid, roots as well as leaves correspondingly absorb smaller amounts of salt ions. The enhanced finding shows the significance of jasmonic acid in oxidative balancing based on the decreased root growth of plants and the enhanced ATPase functionality of the cytoplasm (Munné-Bosch et al. 2007). Studies on plants have shown that, as tomato research has shown, there is a direct correlation between plant cell concentrations of jasmonic acid and cold tolerance. Plant scientists suggest developing management strategies to increase plant productivity under abiotic stress circumstances. Exogenous phytohormones are a more appealing way to counteract the detrimental effects of abiotic stresses on vegetable yield (Moradmand et al. 2015). Plant researchers are paying close attention to phytohormones because of their multipurpose behavior against various adverse conditions. Higher yields can be achieved by using phytohormones in horticultural crops that are cultivated during abiotic stressors (Table 3).

5. PGPR Triggers Abiotic Stress Tolerance in Horticultural Crops

PGPR are the rhizosphere bacteria that promote plant growth in different ways such as phosphate solubilization, exhibiting antifungal properties, induction of systemic tolerance, and generation of bioactive compounds. PGPR directly impacts plant growth, seed development, and crop yields. The synthesis of secondary molecules such as minerals, riboflavin, and phytohormones may be directly hindered by the growth promotion of plants by PGPR (Jaiswal et al. 2021). These either increase food availability or promote cell division as well as expansions to promote the growth of plant components (Bhattacharyya and Jha, 2012). The primary way that PGPR improves plant nutrition is to boost phosphorus absorption through the solubilization or decomposition of either organic or inorganic phosphatases. Additionally, through the intake of water as well as minerals, they produce organic acids that aid in the availability of different kinds of nutrition (Grobelak et al. 2015). This frequently results in improved plant development. Moreover, PGPR indirectly promotes plant growth by suppressing harmful microbes or root diseases via antibiosis, competition for nutrients such as Fe, and space near plant roots. The effects of commercial biological inoculants on squash development under salt stress in greenhouse conditions were studied by Yildirim et al. (2006). Compared with untreated plants exposed to salt stress, biological treatments significantly increased fresh weight. Moreover, the K^+/Na^+ ratio was increased by the most effective biological inoculants, indicating a positive association between ionic homeostasis and improved stress tolerance, and suggesting a potential strategy for mitigating salt-induced damage in plants. The effects of salt stress through altered mineral uptake (Yildirim et al. 2008). Similar findings were also obtained radish (Kaymak et al. 2009). PGPR inoculation has positive impacts on strawberry growth and yield in salinized environments. Bacterial inoculation of the roots also markedly reduced the permeability of membranes. Furthermore, compared to the 35 mM NaCl implementation with no inoculation, the nitrogen level in leaves was substantially increased by bacterial treatments, while the contents of Cl- and Na+ in leaves, as well as Cl- in roots, decreased substantially due to root infection throughout the bacterial treatments (Karlidag et al. 2011).

Table 3. Exogenous phytohormone supplementation enhanced abiotic stress tolerance in horticulture crops.

Species	Hormone	Stress type	Findings	Reference
Cucumber	SA	Drought	Increased chlorophyll content, reduced oxidative damage, and enhanced antioxidant defense system	Baninasab, (2010)
Tomato	BRs	Cadmium	Reduced cadmium accumulation and increased photosynthetic activity and pigment content	Ahammed et al. (2013)
Melon	JA	Drought	Reduced stomatal aperture, enhanced drought stress tolerance, and jasmonic acid accumulation	Xing et al. (2020)
Calendula	SA	Salinity	Reduced oxidative damage, and increased number of flowers, leaf area, and yield-related parameters	Bayat et al. (2012)
Cucumber	BRs	Salinity	Improved photosynthetic assimilation rate, and antioxidant activity	Yang et al. (2019)
Strawberry	SA	Drought	Enhanced drought stress tolerance, and reduced membrane damage by reducing toxic substances	Sun et al. (2013)
Cucumber	BRs	Metals	Increased AOX activity, BRs biosynthesis, enhanced stress tolerance in plants	Wei et al. (2015)

SA = salicylic acid, BRs = brassinosteroids, JA = jasmonic acid, and AOX = alternative oxidase

5. Conclusion and Future Horizon

The functioning of intricate signaling pathways within the cell is necessary for controlling the development and growth of plants under abiotic stresses. Different stress mitigants have the potential to mitigate various abiotic stresses. These multipurpose stress mitigants significantly change the energy flows throughout the plant cell to produce a more resistant morphology under stress. Phytohormones are important in stress reduction processes throughout the entire crop development process, from seed germination to senescence. Exogenous application of phytohormones has emerged as a promising approach for improving crop production, supported by increasing evidence on the beneficial roles of signaling molecules, phytohormones, and plant growth-promoting rhizobacteria in horticultural crops. It is going to be possible to produce cultivars that may be resistant to abiotic challenges by comprehending the process of interaction/crosstalk of phytohormones mediated by various transcriptional factors.

Abiotic stresses are reducing crop productivity globally. Signaling molecules, phytohormones, and plant growth-promoting rhizobacteria contribute to the lessening of numerous climate-related stresses through inhibition of membrane leakage, enhanced photosynthetic action, restriction of chlorophyll degradation, phytohormonal activation, better root morphology, gene expression, and boost several antioxidant enzymes in horticulture crops. Hence, exploring the biochemical mechanism of plants can help grow resilient cultivars that can grow more productively and with superior yield under stressful conditions using different signaling molecules, phytohormones, and plant growth-promoting rhizobacteria.

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AM and HMDM drafted the outline of the manuscript. Ans Mujahid wrote the initial draft of the manuscript. HMDM revised the manuscript to present form.

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