**Next generation plant hormones in abiotic stress tolerance**

**Abstract**

Abiotic stressors such as drought, salinity, extreme temperatures and heavy metal toxicity, represent significant obstacles to global agricultural productivity. Next generation plant hormones including Jasmonic Acid (JA), Strigolactones (SLs) and Melatonin, have been identified as essential regulators of stress adaptation. These hormones are instrumental in modulating stress-responsive signaling pathways thereby enhancing plant resilience through various physiological and molecular mechanisms. Jasmonic Acid (JA) serves as a vital hormone in plant defense, orchestrating responses to oxidative stress, facilitating stomatal closure and promoting the production of secondary metabolites to counteract drought and salinity stresses. Strigolactones (SLs) influences root architecture and symbiotic relationships, thereby improving water and nutrient absorption in nutrient-deficient and saline environments. Melatonin, recognized for its potent antioxidant properties and role as a signaling molecule, mitigates oxidative damage, optimizes photosynthetic efficiency, and boosts tolerance to abiotic stress through interactions with abscisic acid (ABA) and auxins. The application of advanced biotechnological tools, such as CRISPR/Cas genome editing and nanoparticle-based hormone delivery systems, presents new opportunities for refining hormone regulation in crops. A comprehensive understanding of the interactions between JA, SL, and melatonin with other plant hormones will facilitate the development of stress-resilient crops. These cutting-edge strategies hold significant potential for improving agricultural productivity and sustainability in response to the stresses induced by climate change.

**Keywords**: Abiotic stress, Plant hormones, Resilient, Agricultural productivity, Jasmonic Acid (JA), Melatonin, Strigolactones (SLs)

**Introduction:**

For plants, biotic and abiotic stressors have a significant impact on growth and development. Drought, salt, water logging, heat, cold, and heavy metal stress are examples of abiotic variables (Zahid *et al.,* 2023; Salam *et al.,* 2022; Afridi *et al.,* 2019; Salam *et al.,* 2022). Osmotic stress brought on by drought stress leads plant cells to become dehydrated, which ultimately kills the plant [Salam*et* *al., 2022;].* Additionally, plants' osmoregulation mechanism is severely harmed by salinity. The growth and species distribution of numerous plant communities are impacted by waterlogging stresses, also referred to as flooding stress (Voesenek *et al.,* 2004). Plant development is adversely affected by heat and cold stressors. Because it impacts plant growth and development, which in turn affects food safety and security, heavy metal toxicity is the most concerning of them. Metals and metalloids classified as heavy metals have higher generally greater than 5 g/cm3 [Hawkes., 1997]. When these metals are taken up and absorbed by the roots of plants, they can lead to a variety of issues for the plants, including unbalanced electrolytes, electron transport chains, and altered redox homeostasis [Sirhindi *et al., 2020*]. The health of plants and people is seriously threatened by the constantly shifting global climate. Therefore, in order to overcome environmental issues and protect food security and food safety, it is imperative to contend with changing climatic conditions [Wang, F *et al., 2019;* Oshita, *et al.,* 2023; Munir, *et al.,* 2023;]. Plant Metabolic pathways, such as REDOX activities, which enable them to generate their food in the form of ATPs, are often necessary for growth and development [Ahmad,*et al.,*2020;]. However, the presence of heavy metals in the soil, such as copper, arsenic, zinc, cobalt, chromium, manganese, etc., eventually disrupts plant metabolism, which inhibits plant growth [Zeeshan, *et al*., 2023; Azhar, *et al*., 2023; Khan, *et al.,* 2021; Yang, *et al*., 2021; Zeeshan, *et al*., 2021; Salam, *et al*., 2023;]. Due to their extreme insoluble nature, these heavy metals persist in the soil for extended periods of time. Heavy metals enter through roots during the water uptake process cells into the xylem, impeding metabolic processes in plants and ultimately resulting in cell death [Piotrowska*, et al*., 2009;]. It is well known that phytohormones control plant growth and development and promote stress tolerance in response to the aforementioned challenges. One of the most important hormones among them is jasmonic acid (JA), which plays a part in plant signaling pathways that can cause physiological and biochemical changes and assist plants in reducing the deadly impacts of different abiotic stresses [Zuo, *et al*., 2023;]. The precise function of endogenous and exogenous JA in protecting plants from abiotic stressors has been the subject of numerous investigations. However, comprehending the intricate mechanisms governing the synthesis and operation of jain plants is an extremely difficult process with many complex steps and molecular pathways. The production of JA is carefully regulated by the activation of many gene activities. We still don't fully grasp the underlying processes that underlie this activity, though. However, it is crucial to gain a thorough understanding of JA, especially its function in promoting stress tolerance. Gaining a thorough understanding of JA production, its mechanism of action, and its real-world applications is the main goal of this review. As part of our review, we will go into more detail about the intricate mechanisms, production, and function of JA in preventing several abiotic stressors.

**Effects of abiotic stress on horticultural crop productivity**

Plants encounter a variety of stressors throughout their life cycles, beginning with seed germination (Figure 1). Numerous abiotic stresses reduce crop productivity and quality, which results in crop losses products, such as stressors caused by heat, drought, salinity, and nutritional deficiencies (Andreotti, 2020). Abiotic stressors cause morphological, physiological, and biochemical changes in products, which affects not just yield but also product quality (Rao *et al.,* 2016). Horticultural crops face a number of abiotic challenges due to recent changes in the climate. Another major issue facing the agriculture sector in the future is the changing climate (Gao *et al*., 2022; Francini and Sebastiani, 2019; Shahid *et al*., 2021). Plants have been shown to exhibit a variety of stress responses, such as a decrease in the production of photosynthetic machinery, leaf water potential, membrane integrity, photosynthetic pigments, yield and plant growth (Ullah *et al.,* 2018). Additionally, 90 percent of agricultural fields are affected by one or more stress situations. As a result, the horticulture industry is constantly looking for innovative agronomic instruments that can counteract the negative effects of environmental conditions while preserving the production's overall sustainability and quality.

(Source: Zheng et al., 2023)

Fig 1 : A variety of stressors are encountered by plant throughout their life cycles

****

**Jasmonic Acid-Mediated Abiotic Stress Responses:**

Plant tolerance to abiotic stress is tightly linked to the plant signaling chemical jasmonic acid. JA often plays a role in physiological and molecular reactions to abiotic stress. The antioxidant system (superoxide anion radical, peroxidase, etc.) is frequently activated as part of physiological reactions. NADPH-oxidase)[Karpets, *et al*.,2014] buildup of soluble carbohydrates and amino acids (isoleucine and methionine)[Wasternack, *et al*., 2014], and control of stomatal opening and closure[Acharya, *et al.,* 2009]. JA-associated genes (JAZ, AOS1, AOC, LOX2, and COI1) are expressed [Hu,Y.R *et al*., 2017; Robson, *et al.,* 2010], interact with other plant hormones (ABA, ET, SA, GA, IAA, and BR) [Ku, *et al*., 2018; Yang, *et al*., 2019], and interact with transcription factors (MYC2 and bHLH148) [Zhao, *et al*., 2013; Seo, *et al*, 2011]. Figure 2 illustrates potential JA pathways in abiotic stress tolerance. The function of JA signaling in controlling plant responses in various settings is covered in this section.

Fig 2 : Illustrating the potential JA pathways in abiotic stress tolerance



(Source: Jia Wang, *et al*., 2020)

**Cold Stress:**

Plant growth and development are significantly hampered by low temperature stress, which also has a significant impact on the geographic spread of plants. Low temperature stress, which is defined as plant damage brought on by temperatures above and below zero, can take two different forms: chilling stress and freezing stress. C, in that order [Huang, *et al*., 2014; Trischuk, *et al*., 2014]. In order to stabilize the ensuing cell membrane damage, plants have developed sophisticated tolerance mechanisms against such stressors, such as the activation of hormone-related genes and the accumulation of proteins, amino acids, and soluble carbohydrates linked to cold-induced stress[Hincha, *et al*., 2014]. Genes involved in JA biosynthesis, such as lipoxygenase2 (LOX2), allene oxide synthase1 (AOS1), and allene oxide cyclase (AOC), can be expressed under low temperature settings. In order to improve cold tolerance, jasmonic acid upregulates the transcriptional pathway for C-repeat binding factor (CBF), which in turn positively influences downstream cold-responsive genes [Hu, *et al*., 2017].Recent research on Bananas have demonstrated that during cold storage, two MYC2 TFs are quickly activated by the exogenous administration of MeJA. Furthermore, MeJA dramatically increases the expression of genes involved in the cold-responsive pathway that promote CBF expression (ICE-CBF) [Zhao, *et al*., 2013]. These results show that, in concert with MaICE1, the MaMYC2 transcription factor contributes to MeJA-induced chilling tolerance in banana fruit. Furthermore, exogenous JA therapy can boost antioxidant production and decrease lipoxygenase activity to improve plants' resistance to cold. Boost antioxidant production and lipoxygenase activity to improve plants' resistance to cold. Furthermore, Lietal.[Li, *et al*., 2018]observed that the expression of CBF, late embryogenesis abundant (LEA), anddehydration-responsive element binding (DREB1), as well as ABA and JA concentrations, rose in Zoysia japonica under chilling stress. Additionally, Cao et al. [Cao*, et al.,* 2009] discovered that during the storage of MeJA-treated loquat fruit, the activities of the enzymes superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) rose whereas lipoxygenase activity fell.

**Drought Stress:**

Global warming and increasingly frequent and/or severe drought episodes in many significant agricultural regions throughout the world are being caused by climate change. One of the main causes of crop yield loss and even crop failure is the effect of drought stress on crops, which can cut yields from several crops by more than 50% [Abdullah, *et al*., 2015]. Suppressed plant growth [Sun, *et al*., 2017; Javed, *et al.,* 2011], decreased photosynthetic rates [Huang, *et al*., 2017], and hastened leaf senescence [Munne-bosch, *et al*., 2004; Ma, *et al*., 2018] are the overall effects of drought stress. Furthermore, oxidative reactions, membrane lipid buildup, and the production of antioxidant enzymes can all be brought on by drought stress [Lei, *et al*., 2008; Wang, *et al*., 2014]. By controlling stomatal opening and shutting in Arabidopsis thaliana, jasmonic acid can reduce water loss [Savchenko, *et al*., 2014]. The concentrations of endogenous JAs increase rapidly following drought stress, and then return to the baseline levels if stress periods are extended. Furthermore, during drought stress, a large number of genes and transcription factors linked to drought stress are expressed. In the JA signaling pathway, jasmonate ZIM-domain proteins (JAZ) function as regulators, usually repressors. OsJAZ1 has been shown by Fu et al. [Fu*, et al*., 2017] to have a negative regulatory function in rice drought stress tolerance, specifically with regard to the ABA and JA signaling pathways. Additionally, OsbHLH148, a basic helix–loop–helix protein, was discovered by Seo et al. [Seo*, et al.,* 2011] to function as a transcriptional regulator and upregulate OsDREB1 and OsJAZ, which are implicated in the JA signaling pathway and drought stress responses, respectively. Additionally, Ge et al. [Ge*, et al*., 2010] found that temporary JA buildup in a genotype of Prunus armeniaca that is drought-tolerant may enhance plant survival under soil drought conditions, encourage leaf senescence, and stop excessive water loss. On the other hand, P. armeniaca damage linked to drought stress may be mitigated by the exogenous administration of JAs. MeJA applied topically to soybean leaves can improve their ability to withstand water stress, and additional research revealed higher concentrations of sugars, phenolic compounds, and flavonoids [Mohamed, *et al.,* 2017]. These results suggest that plants' ability to withstand drought stress is influenced by both endogenous and exogenous JAs.

**Salt Stress:**

Plant metabolism is disrupted by salt stress, which can result in oxidative stress, genotoxicity, membrane problems, and malnourishment [Syeed, *et al*., 2011; Kadri, *et al*., 2014]. Plants' ability to withstand salt stress can be improved by both endogenous and exogenous JA [Domenico, *et al*., 2019]. Changes in tomato cultivars' endogenous JAs during salt stress were examined by Pedranzani et al. [Pedranzani*, et al*., 2003]. Their results showed that salt stress tolerance, not JA production, was linked to the variation in lipid kinase activity between the two salt-tolerant cultivars under investigation. According to Abouelsaad et al. [Abouelsaad, *et al*., 2018], endogenous JA improved tomato salt tolerance mostly by maintaining balance among reactive oxygen species (ROS). Nevertheless, other research has shown that exogenous JA treatments enhanced photosynthetic rates, proline contents, ABA levels, and antioxidant enzyme activity [Bandurska, *et al*., 2003; Walia, *et al*., 2007] to lessen salt-induced damage to a variety of plants. possibly by decreases in the rates at which Na+ accumulates in shoots [Khan, *et al*., 2012]. By reducing Na+ uptake, exogenous JA was found by Shahzad et al. [Shahzad, *et al*., 2015] to enhance Na+ exclusion in the root and promote surface salt stress resistance in two genotypes of maize. JA levels rise during the initial stages of salt stress and may play an indirect role in the suppression of leaf development in genotypes that are susceptible to salt. According to Qiu et al. [Qiu*, et al.,* 2014], three days of exogenous JA treatment dramatically reduced the levels of hydrogen peroxide (H2O2) and malondialdehyde (MDA) in wheat seedlings, increasing the plants' resistance to salt stress. Transcript levels and the activity of SOD, peroxidase, CAT, and APX also increased dramatically. These findings suggest that by raising the levels of antioxidant molecules and antioxidant enzyme activity, JA may help people tolerate salt stress.

**Heavy Metal Stress**

In addition to polluting the environment, heavy metals hinder the growth and development of plants [Zhang, *et al.,* 2018]. When Suaeda glauca and A. thaliana were subjected to elevated levels of lead (Pb), nickel (Ni), cadmium (Cd), and manganese (Mn), their fresh weight and concentrations of photosynthetic pigments both dropped. Even at very low concentrations, many of these metals may be harmful to plants and serve no useful purpose in them [Ali, *et al*., 2012]. Cd concentrations in roots and leaves rose significantly at increasing doses of CdCl2, especially in spr2 plants, according to Zhao et al.'s comparison of Cd stress responses in wild-type and JA-deficient mutant spr2 tomatoes [Zhao, *et al*., 2016]. The findings showed that tomato seedlings' sensitivity to Cd may be increased by a lack of endogenous JA. Furthermore, as stated by Sirhindi et al. [Sirhindi, *et al*., 2015], To increase Glycine max seeding tolerance to Ni2+ stress, exogenous JA administration before to NiCl2 stress may be beneficial. Azeem [Azeem, *et al*., 2018] also showed that exogenous supplementation of JA reduced the negative effects of oxidative stress on growth, biomass production, and protein concentrations in Ni-treated plants by further increasing antioxidant enzyme activity. They also showed that JA protected the seedlings by controlling the antioxidant machinery and safeguarding DNA synthesis of total proteins. In addition to increasing osmotic and antioxidant activity, external JA supplementation may reduce CD accumulation rates in faba bean roots, shoots, and leaves by preventing H2O2 and MDA accumulation [Noriega, *et al.,* 2012]. According to Noriega et al. [Carvalho, *et al.,* 2013], JA activated the antioxidant machinery of glutathione or ascorbate, which in turn decreased the activity of lipid peroxidase. Furthermore, ROS homeostasis may be the only factor regulating the notable rise in HO-1 antioxidant enzyme activity that they saw during heavy metal stress. These results suggest that via controlling their antioxidant systems, JAs control how plants react to heavy metal stress.

**Role of melatonin in plants under abiotic stress:**

**Salinity stress:**

Melatonin has been shown in published studies to reduce abiotic stress in a variety of crop plant species. According to (Yin *et al*. 2019), salt stress increased ROS activity and photoperiod regulation while decreasing chlorophyll concentration and photosynthetic activity. By strengthening plants' antioxidant defense mechanisms, melatonin enhanced photosynthetic activity, promoted the growth of green bean seedlings under salt stress, and reduced oxidative damage brought on by ROS (Elsayed *et al.,* 2021; Hasanuzzaman *et al*., 2020). According to several research, melatonin is essential for different plant species' adaptation responses to salt stress (Liang *et al*., 2018; Chen *et al*., 2018). Nevertheless, the majority of these investigations are observational, and neither physiological nor molecular study has substantiated the findings (Liu *et al.*, 2020). Melatonin increased salt stress in rice by facilitating K+ retention (a crucial part of plant tissue tolerance mechanisms) in the roots of plants and by facilitating the process that needed ROS signaling dependent on Oryza sativa (OS) respiratory burstoxidase homolog F (OsRBOHF) to activate stress-responsive genes, which in turn boosted the expression of K+ uptake transporters, especially OsHAK5, in the root tips (Liu *et al*., 2020). Salt stress has been shown to reduce potassium, an element that is crucial for plant growth and development (Chen *et* *al*., 2018; Liu *et al*., 2019). These outcomes are consistent with Huang *et al*.'s (2019) findings. He suggested that stress signaling and plant adaptation to saline stress may depend on the generation of H2O2 mediated by respiratory burst oxidase homolog (RBOH) produced by NaCl. However, because they haven't been carried out on a wide range of plants under abiotic stressors, research on the function of OsRBOHF-dependent ROS signaling in the activation of stress sensitive genes and enhanced expression of K+ uptake transporters in the root tip of plants is limited. To enhance the uptake of K+ transporter ions in the root tips of various crops under varied stressors, additional study should concentrate on discovering responsive genes from OsRBOHF-dependent ROS signaling (Yu *et al.,* 2018).

**Drought stress:**

Crop yields decline as a result of drought stress's detrimental effects on plants' morphophysiological and biochemical activity (Chen *et al*., 2019; Singh *et al*., 2015). Oxidative stress is caused by drought stress, which also damages plant cells and impairs antioxidant defense systems by reducing stomatal closure and photosynthetic activity through increased ROS buildup. Since it causes electron leakage, lipid peroxidation, and consequent membrane damage in addition to damaged protein and nucleic acid contents, the buildup of ROS is regarded as a hazard to plant cell viability (Maksup *et al.,* 2014). Plants have evolved a number of mechanisms to control their development in response to varying environmental stressors in order to avoid this harm (Kim and Kim, 2020). Melatonin, a novel regulator of plant growth, is believed to play a role in drought stress reactions (Zhang *et al.,* 2015; Li *et al*., 2021). Plant morphological activity, particularly that related to leaf growth and the relative water conductivity of maize seedlings, was decreased by drought stress. In the meantime, melatonin treatment greatly increased leaf size and relative water conductivity (Li *et al*., 2021). Ye *et al*. (2016) found that melatonin increased the shoot dry weight and leaf size of maize seedlings, which was a comparable outcome. In plants, physiological processes in leaves, such as photosynthesis, respiration, and transpiration, are maintained by stomata, the opening and closing of which are controlled by complex signal transduction pathways and water balance. In the presence of drought stress, plants regulate their cellular moisture content by regulating stomatal closure and reducing their transpiration rate. However, the density of stomata significantly increases with the contraction of guard cells, and deteriorates under drought stress (Xue *et al.,* 2021). In general, the application of melatonin has shown resistance against the deterioration of stomata cells and increased its length and width under drought stress in corn (Li *et al*., 2021). The contrasting results in the study by Li *et al.* (2015), showed, however, that apples' stomatal cell density was unaffected by drought stress. However, the stomata remained open and the turgor pressure remained high due to the exogenous melatonin administration. distinct plant species may have distinct melatonin regulation mechanisms, which could account for the discrepancy in the results (Li *et al*., 2021). The current research shows that while the amount, effectiveness, and mechanisms of action of melatonin vary among plant species, fewer morphophysiological reactions have been observed in several plants during drought stress.

**Heat stress:**

Elevated levels of heat stress lead to an increase in endogenous melatonin levels, which, in turn, boosts thermotolerance due to melatonin's strong antioxidant properties in plants (Liang *et al*., 2018; Ahammed *et al.,* 2019). A prior investigation on Arabidopsis demonstrated that melatonin raised the seed germination rate from about 30% to 39% in the presence of heat stress (Hernandez *et al*., 2015). The correlation between phytomelatonin production and seed germination has been established, showing that phytomelatonin is produced during the germination of cucumber seeds, with its highest levels occurring 14 hours post-germination (Zhang *et al.,* 2014). However, additional studies on a variety of crops remain necessary. Melatonin enhanced the ability to germinate by facilitating the use of soluble sugars and the production of new proteins**.** and increased amylase and a-amylase activities in melon and Limonium bicolor seeds (Castañares and Bouzo, 2019; Li *et al*., 2019). Melatonin considerably lessens the negative effects of heat stress on plant seedlings, according to recent studies. First, because of the high potency of melatonin, it maintained high viability and germination capacity (Hernandez *et al.,* 2015). When plants are exposed to high levels of heat stress, the activities of antioxidant enzymes, such as superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT), are increased (Wang *et al*., 2022), and melatonin inhibits the accumulation of H2O2 (Marta et al., 2016). Genes involved in gibberellin (GA) production, such as GA20ox and GA3ox, are up-regulated in response to melatonin administration. Melatonin also raises the content of GA, especially GA4. Unfortunately, the important gene NECD2, which is primarily involved in ABA biosynthesis, has its expression down-regulated by melatonin (Zhang *et al*., 2014; Li *et al*., 2019). More research should be done on the mechanisms underlying the up- and down-regulation of gene expression in plant cells during heat stress. Additionally, heat stress can upset the antioxidant equilibrium, which leads to the buildup of ROS and peroxidative damage to cell membranes (Sun *et al.,* 2021). The negative effects of heat stress on plant shoot and root growth were reversed in rice and tomatoes when melatonin was applied exogenously (Wang *et al.,* 2018). By controlling redox homeostasis and modifying NO and polyamine production in tomato seedlings, melatonin also lessened the harm brought on by heat stress (Jahan *et al*., 2019). Melatonin-mediated heat stress in Arabidopsis plants was lessened by the heat shock protein HSP90 and heat shock factors, such as HSFA2 and HSFA32 (Shi *et al*., 2015a). According to a study, HSPs stopped tomatoes' heat-stressed cellular proteins from refolding or breaking down denatured proteins (Xu *et a*l., 2016).

**Cold stress:**

Cold stress is one of the major abiotic stresses that reduces crop growth and yield, especially in temperate zones and highly elevated areas (Bhat *et al*., 2022). Plants exposed to cold stress experience changes in various physiological, molecular, metabolic, and Ahmad et al. biochemical activities. Examples include variations in membrane fluidity, metabolism homeostasis, and enzyme activity (Wu *et al*.,2022). Photosynthesis is a pivotal plant metabolism process, and one that is highly sensitive to cold stress. This is because low temperature hinders many major components of photosynthesis (Dahal *et al*.,2012). Chlorophyll content decreases under cold stress, leading to chlorosis in leaves (Kaura *et al.*, 2022). The chlorophyll content of leaves provides important information about the effectiveness of physiological processes in plants in plants (Gitelson *et al.*, 2003). Plants treated with melatonin had a higher concentration of chlorophyll than non-treated plants under cold stress (Yang *et al*.,2022). Plant growth at low temperatures induces the excessiveproduction or inefficient deactivation of ROS, such as H2O2, superoxide anions (i.e., O2–), and hydroxyl radicals (i.e., OH), which in turn can cause injury to plants (Ghaderian *et al.*, 2015). In addition, ROS accumulation causes the oxidation of proteins and peroxidation of lipids within plant cells, resulting in reduced plant growth (Nahar *et al*., 2015). Several studies have demonstrated that exogenous melatonin can stimulate plant growth in various plants, such as corn, and can promote the germination of cucumber seeds under cold stress (Kolodziejczyk *et al*., 2016; Posmyk *et al.,* 2009b). In Arabidopsis plants, melatonin modulates leaf senescence against cold stress (Shi *et al*., 2015b). Melatonin applications enhance the resistance of Bermuda grass to cold stress by improving cell membrane stability, and by regulating photosynthesis and metabolic activity (Khalid *et al*., 2022). Melatonin played a role as both a first-line defense and internal sensor of oxidative stress in a study of different species of plants (Iqbal and Khan, 2022). For example, in barley, exogenous melatonin can enhance photosynthetic carbon assimilation by improving the plant antioxidant defense systems of organelles under cold stress (Li *et al.,*2016). Therefore, the improved performance of primed seeds in terms of seedling growth and germination might be the result of improved antioxidant defense systems under cold stress (Cao *et al.*, 2022). However, an understanding of the growth of waxy corn and other crop seeds primed with melatonin in response to cold stress is still limited (Cao *et al*., 2022).

**Strigolactones:**

**Role of strigolactones under high temperature**

Crops that are resistant to a range of environmental stressors are being developed using SLs. Importantly, SLs have been described as a helpful tool for stress-related events, and their role in some environmental difficulties has been noted (Tariq *et al*., 2023). Unintentional heat waves and global warming are two significant environmental issues that have gained attention recently. Severe climate change may result in temperatures higher than ideal, endangering tree populations and maybe damaging crops. In 2021, Shafqat et al. Long-term or short-term temperature fluctuations may cause stress for the plant, which requires a specific range of temperatures to carry out its physiological (Khan *et al*., 2019) and biochemical functions (Bermudez *et al*., 2021). SLs are advantageous regulators of the body's resistance to heat stress because of their capacity to increase the activity of antioxidant enzymes and the transcription of proteins (Chi *et al.*, 2021). For plants to adjust to temperature stressors, SLs signaling and biosynthesis are crucial (Pandey *et al.,* 2016). Induction of antioxidants in plants is associated with additional defenses against cellular damage caused by temperature stressors. As signaling molecules, SLs serve as both endogenous hormones that control plant growth and constituents of root exudates that promote symbiotic connections between soil microbes and plants.

**Role of strigolactones under drought stress**

In recent years, the intensity of water-related stresses has increased drastically such as drought and salinity, which significantly impacted the plant’s growth and development. These problems are spreading worldwide due to global changes. Drought being chronic abiotic stress is responsible for approximately 70 % of the potential crop loss globally. With a significant change in moisture levels, drought hinders agriculture production worldwide. A major impact on moisture levels is mainly caused by the current trends of global warming which increases the

intensity of drought. By the year 2050, productivity losses are expected to increase by 30 % due to drought stress. The condition where the transpiration of the plants exceeds the water absorbed by the roots due to insufficient precipitation or groundwater level drop is referred to as drought (Khalid *et al*., 2022). When subjected to drought stress the electron transport chain of the plants gets disturbed resulting in oxida tive stress and ROS accumulation leading to the damage of essential organelles. The main objective of the agriculture industry is to provide global food security using a sustainable approach. With the growing population, the challenging demand to feed the population requires high- intensity agriculture management (L´ opez-R´aez, 2015). Currently, the strategies used to cope with stresses to minimize crop losses are mainly focused on genetic engineering and traditional breeding crops to develop resistant cultivars, which are time-consuming and costly. To achieve the food demand, advancement in enhanced drought-tolerant plants, and finding cheaper and sustainable alternatives are urgently required (Khalid *et al*., 2022).

**Conclusion**

Plant hormones are crucial to a plant's growth and development and serve as a vital line of defense against abiotic stress. Hormones alter the growth pattern so that plants can tolerate stress. Numerous hormones, their downstream response factors, related gene networks, and transcription factors are all involved in the plant stress response. Abiotic stress tolerance mediated by phytohormones is largely dependent on the interactions between hormones, whether they are antagonistic or synergistic [Rivero, *et al*., 2010]. It is essential to comprehend how the various pathways governing the stress response interact at the molecular level in order to manipulate them and increase stress tolerance. This is significant because, in the context of a changing global climate, abiotic pressures are becoming more varied, persistent, and intense. Given the limited effectiveness of traditional breeding methods in addressing abiotic stress, plant hormones are a key focus for improved management of this condition. The cultivation of climate-resilient crops can greatly benefit from the involvement of phytohormone pathways and its intermediaries.

Plant bioengineering methods have been helpful in accomplishing this goal; soybeans [Li, *et al.,* 2013], maize [Lu, *et al*., 2013], rice [Zhang, *et al*., 2012 ], and potatoes [Kim, *et al.*, 2013] are a few examples. The hormone-mediated regulatory mechanisms of the plant stress response are being identified using methods such as genome editing, transgenic plants, transcriptome analysis, and next-generation sequencing analysis. Understanding the mechanism of stress tolerance in plants has been aided by transcriptome analysis utilizing microarrays, a survey of transcriptome profiles, and RNA-seq measurements of microRNA levels in stressed plants [Cai*, et al*., 2020]. The CRISPR/CAS system [Osakabe, *et al.,* 2014; Shukla*, et al*., 2009] and specially engineered endonucleases such as zinc finger nucleases (ZFN) or TAL effector nucleases (TALEN; [Osakabe, *et al.,* 2014; Nekrasov, *et al.,* 2013] can now be used to alter genomes in a site-specific way thanks to genome editing technology.

**References:**

1. Zahid, G.; Iftikhar, S.; Shimira, F.; Ahmad, H.M.; Kaçar, Y.A. An overview and recent progress of plant growth regulators (PGRs) in the mitigation of abiotic stresses in fruits: A review. *Sci. Hortic.* **2023**, *309*, 111621.
2. Salam, A.; Khan, A.R.; Liu, L.; Yang, S.; Azhar, W.; Ulhassan, Z.; Zeeshan, M.; Wu, J.; Fan, X.; Gan, Y. Seed priming with zinc oxide nanoparticles downplayed ultrastructural damage and improved photosynthetic apparatus in maize under cobalt stress. *J. Hazard. Mater.* **2022**, *423*, 127021.
3. Afridi, M.S.; Mahmood, T.; Salam, A.; Mukhtar, T.; Mehmood, S.; Ali, J.; Khatoon, Z.; Bibi, M.; Javed, M.T.; Sultan, T.; et al. Induction of tolerance to salinity in wheat genotypes by plant growth promoting endophytes: Involvement of ACC deaminase and antioxidant enzymes. *Plant Physiol. Biochem.* **2019**, *139*, 569–577.
4. Salam, A.; Ali, A.; Afridi, M.S.; Ali, S.; Ullah, Z. Agrobiodiversity: Effect of Drought Stress on the Eco-physiology and Morphology of Wheat. In *Biodiversity, Conservation and Sustainability in Asia: Volume 2: Prospects and Challenges in South and Middle Asia*; Öztürk, M., Khan, S.M., Altay, V., Efe, R., Egamberdieva, D., Khassanov, F.O., Eds.; Springer International Publishing: Cham, Switzerland, 2022; pp. 597–618.
5. Voesenek, L.; Rijnders, J.; Peeters, A.; Van de Steeg, H.; De Kroon, H. Plant hormones regulate fast shoot elongation under water: From genes to communities. *Ecology* **2004**, *85*, 16–27.
6. Hawkes, S.J. What is a “heavy metal”? J. Chem. Educ. 1997, 74, 1374.
7. Sirhindi, G.; Mushtaq, R.; Gill, S.S.; Sharma, P.; Abd\_Allah, E.F.; Ahmad, P. Jasmonic acid and methyl jasmonate modulate growth, photosynthetic activity and expression of photosystem II subunit genes in Brassica oleracea L. Sci. Rep. 2020, 10, 9322.
8. Wang, F.; Yu, G.; Liu, P. Transporter-mediated subcellular distribution in the metabolism and signaling of jasmonates. Front. Plant Sci. 2019, 10, 390.
9. Oshita, T.; Sim, J.; Anee, T.I.; Kiyono, H.; Nozu, C.; Suzuki, N. Attenuation of negative effects caused by a combination of heat and cadmium stress in Arabidopsis thaliana deficient in jasmonic acid synthesis. J. Plant Physiol. 2023, 281, 153915.
10. Munir, R.; Jan, M.; Muhammad, S.; Afzal, M.; Jan, N.; Yasin, M.U.; Munir, I.; Iqbal, A.; Yang, S.; Zhou, W. Detrimental effects of Cdandtemperature on rice and functions of microbial community in paddy soils. Environ. Pollut. 2023, 324, 121371.
11. Ahmad, P.; Alyemeni, M.N.; Al-Huqail, A.A.; Alqahtani, M.A.; Wijaya, L.; Ashraf, M.; Kaya, C.; Bajguz, A.J.P. Zinc oxide nanoparticles application alleviates arsenic (As) toxicity in soybean plants by restricting the uptake of as and modulating key biochemical attributes, antioxidant enzymes, ascorbate-glutathione cycle and glyoxalase system. Plants 2020, 9, 825.
12. Zeeshan, M.; Hu, Y.X.; Guo, X.H.; Sun, C.Y.; Salam, A.; Ahmad, S.; Muhammad, I.; Nasar, J.; Jahan, M.S.; Fahad, S.; et al. Physiological and transcriptomic study reveal SeNPs-mediated AsIII stress detoxification mechanisms involved modulation of antioxidants, metal transporters, and transcription factors in Glycine max L. (Merr.) roots. Environ. Pollut. 2023, 317, 120637.
13. Azhar, W.; Khan, A.R.; Salam, A.; Ulhassan, Z.; Qi, J.; Shah, G.; Liu, Y.; Chunyan, Y.; Yang, S.; Gan, Y. Ethylene accelerates copper oxide nanoparticle-induced toxicity at physiological, biochemical, and ultrastructural levels in rice seedlings. Environ. Sci. Pollut. Res. 2023, 30, 26137–26149.
14. Khan, A.R.; Azhar, W.; Wu, J.; Ulhassan, Z.; Salam, A.; Zaidi, S.H.R.; Yang, S.; Song, G.; Gan, Y. Ethylene participates in zinc oxide nanoparticles induced biochemical, molecular and ultrastructural changes in rice seedlings. Ecotoxicol. Environ. Saf. 2021, 226, 112844.
15. Yang, S.; Ulhassan, Z.; Shah, A.M.; Khan, A.R.; Azhar, W.; Hamid, Y.; Hussain, S.; Sheteiwy, M.S.; Salam, A.; Zhou, W. Salicylic acid underpins silicon in ameliorating chromium toxicity in rice by modulating antioxidant defense, ion homeostasis and cellular ultrastructure. Plant Physiol. Biochem. 2021, 166, 1001–1013.
16. Zeeshan,M.;Hu,Y.X.; Iqbal, A.; Salam, A.; Liu, Y.X.; Muhammad, I.; Ahmad, S.; Khan, A.H.; Hale, B.; Wu, H.Y.; etal. Amelioration of AsV toxicity by concurrent application of ZnO-NPs and Se-NPs is associated with differential regulation of photosynthetic indexes, antioxidant pool and osmolytes content in soybean seedling. Ecotoxicol. Environ. Saf. 2021, 225, 112738.
17. Salam, A.; Rehman, M.; Qi, J.; Khan, A.R.; Yang, S.; Zeeshan, M.; Ulhassan, Z.; Afridi, M.S.; Yang, C.; Chen, N. Cobalt stress induces photosynthetic and ultrastructural distortion by disrupting cellular redox homeostasis in maize. Environ. Exp. Bot. 2023, 2023, 105562.
18. Piotrowska, A.; Bajguz, A.; Godlewska-˙ Zyłkiewicz, B.; Czerpak, R.; Kami´ nska, M.J.E.; Botany, E. Jasmonic acid as modulator of lead toxicity in aquatic plant Wolffia arrhiza (Lemnaceae). Environ. Exp. Bot. 2009, 66, 507–513.
19. Zuo,Z.-F.; Lee, H.-Y.; Kang, H.-G. Basic Helix-Loop-Helix Transcription Factors: Regulators for Plant Growth Development and Abiotic Stress Responses. Int. J. Mol. Sci. 2023, 24, 1419.
20. Andreotti, C. (2020). Management of abiotic stress in horticultural crops: Spotlight on biostimulants. Agronomy 10, 1514. doi: 10.3390/agronomy10101514
21. Rao, N. S., Shivashankara, K. S., and Laxman, R. H. (2016). Abiotic stress physiology of horticultural crops, vol 311 (India: Springer). doi: 10.1007/978-81 322-2725-0
22. Gao, J., Shahid, R., Ji, X., and Li, S. (2022). Climate change resilience and sustainable tropical agriculture: Farmers’ perceptions, reactive adaptations and determinants of reactive adaptations in hainan, China. Atmosphere 13 (6), 955. doi: 10.3390/atmos13060955
23. Francini, A., and Sebastiani, L. (2019). Abiotic stress effects on performance of horticultural crops. Horticulturae 5, 67. doi: 10.3390/books978-3-03921-751-9
24. Shahid, R., Shijie, L., Shahid, S., Altaf, M. A., and Shahid, H. (2021). Determinants of reactive adaptations to climate change in semi-arid region of Pakistan. J. Arid Environments 193, 104580. doi: 10.1016/j.jaridenv.2021.104580
25. Ullah,A., Sun,H.,Yang,X., andZhang,X. (2018).Anovel cottonWRKYgene, GhWRKY6-like, improves salt tolerance by activating the ABA signalling pathway and scavenging of reactive oxygen species. Physiol. Plant 162, 439–454. doi: 10.1111/ppl.12651
26. Karpets, Y.V.; Kolupaev, Y.E.; Lugovaya, A.A.; Oboznyi, A.I. E ect of jasmonic acid on the pro-/antioxidant system of wheat coleoptiles as related to hyperthermia tolerance. Russ. J. Plant Physiol. 2014, 61, 339–346.
27. Wasternack, C. Action of jasmonates in plant stress responses and development—Applied aspects. Biotechnol. Adv. 2014, 32, 31–39.
28. Acharya, B.R.; Assmann, S.M. Hormone interactions in stomatal function. Plant Mol. Biol. 2009, 69, 451–462.
29. Hu,Y.R.; Jiang, Y.J.; Han, X.; Wang, H.P.; Pan, J.J.; Yu, D.Q. Jasmonate regulates leaf senescence and tolerance to cold stress: Crosstalk with other phytohormones. J. Exp. Bot. 2017, 68, 1361–1369.
30. Robson, F.; Okamoto, H.; Patrick, E.; Harris, S.R.; Wasternack, C.; Brearley, C.; Turner, J.G. Jasmonate and phytochrome a signaling in Arabidopsis wound and shade responses are integrated through JAZ1 stability. Plant Cell 2010, 22, 1143–1160.
31. Ku, Y.S.; Sintaha, M.; Cheung, M.Y.; Lam, H.M. Plant hormone signaling crosstalks between biotic and abiotic stress responses. Int. J. Mol. Sci. 2018, 19, 3206.
32. Yang, J.; Duan, G.H.; Li, C.Q.; Liu, L.; Han, G.Y.; Zhang, Y.L.; Wang, C.M. The crosstalks between jasmonic acid and other plant hormone signaling highlight the involvement of jasmonic acid as a core component in plant response to biotic and abiotic stresses. Front. Plant Sci. 2019, 10, 1349.
33. Zhao,M.L.; Wang, J.N.; Shan, W.; Fan, J.G.; Kuang, J.F.; Wu, K.Q.; Li, X.P.; Chen, W.X.; He, F.Y.; Chen, J.Y.; et al. Induction of jasmonate signalling regulators MaMYC2s and their physical interactions with MaICE1 in methyl jasmonate-induced chilling tolerance in banana fruit. Plant Cell Environ. 2013, 36, 30–51.
34. Seo, J.S.; Joo, J.; Kim, M.J.; Kim, Y.K.; Nahm, B.H.; Song, S.I.; Cheong, J.J.; Lee, J.S.; Kim, J.K.; Choi, Y.D. OsbHLH148,abasichelix-loop-helix protein, interacts with OsJAZ proteins in a jasmonate signaling pathway leading to drought tolerance in rice. Plant J. 2011, 65, 907–921.
35. Huang, B.R.; DaCosta, M.; Jiang, Y.W. Research advances in mechanisms of turfgrass tolerance to abiotic stresses: From physiology to molecular biology. Crit. Rev. Plant Sci. 2014, 33, 141–189.
36. Trischuk, R.G.; Schilling, B.S.; Low, N.H.; Gray, G.R.; Gusta, L.V. Cold acclimation, de-acclimation and re-acclimation of spring canola, winter canola and winter wheat: The role of carbohydrates, cold-induced stress proteins and vernalization. Environ. Exp. Bot. 2014, 106, 156–163.
37. Hincha, D.K.; Zuther, E. Plant Cold Acclimation: Methods and Protocols; Springer: New York, NY, USA, 2014; p. 1166.
38. Li,S.M.; Yang, Y.; Zhang, Q.; Liu, N.F.; Xu, Q.G.; Hu, L.X. Di erential physiological and metabolic response to low temperature in two zoysiagrass genotypes native to high and low latitude. PLoS ONE 2018, 13, e0198885.
39. Cao,S.F.; Zheng, Y.H.; Wang, K.T.; Jin, P.; Rui, H.J. Methyl jasmonate reduces chilling injury and enhances antioxidant enzyme activity in postharvest loquat fruit. Food Chem. 2009, 115, 1458–1463.
40. Abdullah, A.S.; Aziz, M.M.; Siddique, K.H.M.; Flower, K.C. Film antitranspirants increase yield in drought stressed wheat plants by maintaining high grain number. Agric. Water Manag. 2015, 159, 11–18.
41. Sun, X.G.; Shi, J.; Ding, G.J. Combined e ects of arbuscular mycorrhiza and drought stress on plant growth and mortality of forage sorghum. Appl. Soil Ecol. 2017, 119, 384–391.
42. Javed, N.; Ashraf, M.; Akram, N.A.; Ai-Qurainy, F. Alleviation of adverse e ects of drought stress on growth and some potential physiological attributes in Maize (Zea mays L.) by seed electromagnetic treatment. Photochem. Photobiol. 2011, 87, 1354–1362.
43. Huang,J.; Chen, C.; Zhang, W.X.; Ding, C.J.; Su, X.H.; Huang, Q.J. E ects of drought stress on anatomical structure and photosynthetic characteristics of transgenic JERF36 Populus alba P. berolinensis seedling leaves. Sci. Silvae Sin. 2017, 119, 384–391.
44. Munné-bosch, S.; Alegre, L. Die and let live: Leaf senescence contributes to plant survival under drought stress. Funct. Plant Biol. 2004, 31, 8808–8818.
45. Ma, X.Q.; Zhang, J.; Burgess, P.; Rosso, S.; Huang, B. Interactive e ects of melatonin and cytokinin on alleviating drought-induced leaf senescence in creeping bentgrass (Agrostis stolonifera). Environ. Exp. Bot. 2018, 145, 1–11.
46. Lei, Y. Physiological responses of Populus przewalskii to oxidative burst caused by drought stress. Russ. J. Plant Physiol. 2008, 55, 857–864.
47. Wang, L.; He, J.; Ding, H.D.; Liu, H.; Lv, B.; Liang, J.S.; Wang, L.; He, J.; Ding, H.D.; Liu, H.; et al. Overexpression of AT14A confers tolerance to drought stress-induced oxidative damage in suspension cultured cells of Arabidopsis thaliana. Protoplasma 2014, 252, 1111–1120
48. Savchenko, T.; Kolla, V.A.; Wang, C.Q.; Nasafi, Z.; Hicks, D.R.; Phadungchob, B.; Chehab, W.E.; Brandizzi, F.; Froehlich, J.; Dehesh, K. Functional convergence of oxylipin and abscisic acid pathways controls stomatal closure in response to drought. Plant Physiol. 2014, 164, 1151–1160.
49. Fu,J.;Wu,H.;Ma,S.Q.;Xiang,D.H.;Liu,R.Y.;Xiong,L.Z.OsJAZ1attenuatesdroughtresistancebyregulating JA and ABAsignaling in Rice. Front. Plant Sci. 2017, 8, 1–13.
50. Ge, Y.X.; Zhang, L.J.; Li, F.H.; Chen, Z.B.; Wang, C.; Yao, Y.C.; Han, Z.H.; Zhang, J.; Shi, Z.S. Relationship between jasmonic acid accumulation and senescence in drought-stress. Afr. J. Agric. Res. 2010, 5, 1978–1983.
51. Mohamed,H.I.; Latif, H.H. Improvement of drought tolerance of soybean plants by using methyl jasmonate. Physiol. Mol. Biol. Plants 2017, 23, 545–556.
52. Syeed, S.; Anjum, N.A.; Nazar, R.; Iqbal, N.; Masood, A.; Khan, N.A. Salicylic acid-mediated changes in photosynthesis, nutrients content and antioxidant metabolism in two mustard (Brassica juncea L.) cultivars di ering in salt tolerance. Acta Physiol. Plant. 2011, 33, 877–886.
53. Kadri, K.; Abdellaoui, R.; Mhamed, H.C.; Da Silva, J.A.T.; Naceur, M.B. Analysis of salt-induced mRNA transcripts in tunisian local barley (Hordeum vulgare) leaves identified by di erential display RT-PCR. Biochem. Genet. 2014, 52, 106–115.
54. Domenico, S.D.; Taurino, M.; Gallo, A.; Poltronieri, P.; Pastor, V.; Flors, V.; Santino, A. Oxylipin dynamics in Medicago truncatula in response to salt and wounding stresses. Physiol. Plant. 2019, 165, 198–208.
55. Pedranzani, H.; Racagni, G.; Alemano, S.; Miersch, O.; Ramirez, I.; Pena-Cortes, H.; Taleisnik, E.; Machado Domenech, E.; Abdala, G. Salt tolerant tomato plants show increased levels of jasmonic acid. Plant Growth Regul. 2003, 41, 149–158.
56. Abouelsaad, I.; Renault, S. Enhanced oxidative stress in the jasmonic acid-deficient tomato mutant def-1 exposed to NaCl stress. J. Plant Physiol. 2018, 226, 136–144. .
57. Bandurska, H.; Stroi´ nski, A.; Kubi´s, J. The e ect of jasmonic acid on the accumulation of ABA, proline and spermidine and its influence on membrane injury under water deficit in two barley genotypes. Acta Physiol. Plant. 2003, 25, 279–285. .
58. Walia, H.; Wilson, C.; Condamine, P.; Liu, X.; Ismail, A.M.; Close, T.J. Large- scale expression profiling and physiological characterization of jasmonic acid-mediated adaptation of barley to salinity stress. Plant Cell Environ. 2007, 30, 410–421
59. Zhang, X.; Li, M.; Yang, H.H.; Li, X.X.; Cui, Z.J. Physiological responses of Suaeda glauca and Arabidopsis thaliana in phytoremediation of heavy metals. J. Environ. Manag. 2018, 223, 132–139.
60. Ali, I.; Ali, R.; Alothman, Z.A.; Ali, J.; Habila, M.A. Assessment of toxic metals in wheat crops grown on selected soils, irrigated by di erent water sources. Arab. J. Chem. 2012, 9, 1555–1562.
61. Zhao, S.Y.; Ma, Q.F.; Xu, X.; Li, G.Z.; Hao, L. Tomato Jasmonic acid-deficient mutant spr2 seedling response to Cadmium stress. J. Plant Growth Regul. 2016, 35, 603–610.
62. Sirhindi, G.; Mir, M.A.; Sharma, P.; Gill, S.S.; Kaur, H.; Mushtaq, R. Modulatory role of jasmonic acid on photosynthetic pigments, antioxidants and stress markers of Glycine max L. under nickel stress. Physiol. Mol. Biol. Plants 2015, 21, 559–565.
63. Azeem,U.Ameliorating Nickel stress by Jasmonic acid treatment in Zea mays L. Russ. Agric. Sci. 2018, 44, 209–215.
64. Noriega, G.; Cruz, D.S.; Batlle, A.; Tomaro, M.; Balestrasse, K. Heme oxygenase is involved in the protection exerted by Jasmonic acid against Cadmium stress in Soybean roots. J. Plant Growth Regul. 2012, 31, 79–89.
65. Carvalho, R.F.; Campos, M.L.; Azevedo, R.A. The role of phytochromes in stress tolerance. In Salt Stress Plants; Springer: Berlin/Heidelberg, Germany, 2013; pp. 283–299.
66. Yin,Z.,Lu, J.,Meng, S.,Liu,Y.,Mostafa, I.,Qi,M., etal. (2019).Exogenousmelatonin improves salt tolerance in tomato by regulating photosynthetic electron flux and the ascorbate glutathione cycle. J. Plant Interact. 14, 453–463. doi: 10.1080/17429145.2019.1645895
67. Elsayed, A. I., Rafudeen, M. S., Gomaa, A. M., and Hasanuzzaman, M. (2021). Exogenous melatonin enhances the reactive oxygen species metabolism, antioxidant defense-related gene expression, and photosynthetic capacity of phaseolus vulgaris l. @ to confer salt stress tolerance. Physiol. Plant 173, 1369–1381. doi: 10.1111/ppl.13372
68. Hasanuzzaman, M., Bhuyan, M., Zulfiqar, F., Raza, A., Mohsin, S. M., Mahmud, J. A., et al. (2020). Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of a universal defense regulator. Antioxidants 9, 681. doi: 10.3390/antiox9080681
69. Liang, D., Gao, F., Ni, Z., Lin, L., Deng, Q., Tang, Y., et al. (2018). Melatonin improves heat tolerance in kiwifruit seedlings through promoting antioxidant enzymatic activity and glutathione s-transferase transcription. Molecules 23, 584. doi: 10.3390/ molecules23030584
70. Chen, G., Liu, C., Gao, Z., Zhang, Y., Zhang, A., Zhu, L., et al. (2018). Variation in the abundance of OsHAK1 transcript underlies the differential salinity tolerance of an indica and a japonica rice cultivar. Front. Plant Sci. 8, 2216. doi: 10.3389/fpls.2017.02216
71. Liu, J., Shabala, S., Zhang, J., Ma, G., Chen, D., Shabala, L., et al. (2020). Melatonin improves rice salinity stress tolerance by NADPH oxidase-dependent control of the plasma membrane k+ transporters and k+ homeostasis. Plant Cell Environ. 43, 2591 2605. doi: 10.1111/pce.13759
72. Liu, J., Shabala, S., Shabala, L., Zhou, M., Meinke, H., Venkataraman, G., et al. (2019). Tissue-specific regulation of na+ and k+ transporters explains genotypic differences in salinity stress tolerance in rice. Front. Plant Sci. 10. doi: 10.3389/fpls.2019.01361
73. Huang, Y., Cao, H., Yang, L., Chen, C., Shabala, L., Xiong, M., et al. (2019). Tissue specific respiratory burst oxidase homolog-dependent H2O2 signaling to the plasma membrane h+-ATPase confers potassium uptake and salinity tolerance in cucurbitaceae. J. Exp. Bot. 70, 5879–5893. doi: 10.1093/jxb/erz328
74. Yu, Y., Lv, Y., Shi, Y., Li, T., Chen, Y., Zhao, D., et al. (2018). The role of phyto melatonin and related metabolites in response to stress. Molecules 23, 1887. doi: 10.3390/ molecules23081887
75. Chen, J., Li, Y., Luo, Y., Tu, W., and Wan, T. (2019). Drought differently affects growth properties, leaf ultrastructure, nitrogen absorption and metabolism of two dominant species of hippophae in Tibet plateau. Acta Physiol. Plant 41, 1–12. doi: 10.1007/s11738 018-2785-6
76. Singh, R., Mishra, A., Dhawan, S. S., Shirke, P. A., Gupta, M. M., and Sharma, A. (2015). Physiological performance, secondary metabolite and expression profiling of genes associated with drought tolerance in withania somnifera. Protoplasma 252, 1439 1450. doi: 10.1007/s00709-015-0771-z
77. Maksup, S., Roytrakul, S., and Supaibulwatana, K. (2014). Physiological and comparative proteomic analyses of Thai jasmine rice and two check cultivars in response to drought stress. J. Plant Interact. 9, 43–55. doi: 10.1080/17429145.2012.752042
78. Kim, S., and Kim, T.-H. (2020). Alternative splicing for improving abiotic stress tolerance and agronomic traits in crop plants. J. Plant Biol. 63, 409–420. doi: 10.1007/ s12374-020-09282-2
79. Li, C., Tan, D.-X., Liang, D., Chang, C., Jia, D., and Ma, F. (2015). Melatonin mediates the regulation of ABA metabolism, free-radical scavenging, and stomatal behaviour in two malus species under drought stress. J. Exp. Bot. 66, 669–680. doi: 10.1093/jxb/eru476
80. Zhang, N., Sun, Q., Zhang, H., Cao, Y., Weeda, S., Ren, S., et al. (2015). Roles of melatonin in abiotic stress resistance in plants. J. Exp. Bot. 66, 647–656. doi: 10.1093/jxb/ eru336
81. Li, Z., Su, X., Chen, Y., Fan, X., He, L., Guo, J., et al. (2021). Melatonin improves drought resistance in maize seedlings by enhancing the antioxidant system and regulating abscisic acid metabolism to maintain stomatal opening under PEG-induced drought. J. Plant Biol. 64, 299–312. doi: 10.1007/s12374-021-09297-3
82. Ahammed, G. J., Xu, W., Liu, A., and Chen, S. (2019). Endogenous melatonin deficiency aggravates high temperature-induced oxidative stress in solanum lycopersicum l. Environ. Exp. Bot. 161, 303–311. doi: 10.1016/j.envexpbot.2018.06.006
83. Hernandez, I. G., Gomez, F. J. V., Cerutti, S., Arana, M. V., and Silva, M. F. (2015). Melatonin in arabidopsis thaliana acts as plant growth regulator at low concentrations and preserves seed viability at high concentrations. Plant Physiol. Biochem. 94, 191–196. doi: 10.1016/j.plaphy.2015.06.011
84. Zhang, H. J., Zhang, N., Yang, R. C., Wang, L., Sun, Q. Q., Li, D. B., et al. (2014). Melatonin promotes seed germination under high salinity by regulating antioxidant systems, ABA and GA 4 interaction in cucumber (C ucumis sativus l.). J. Pineal Res. 57, 269–279. doi: 10.1111/jpi.12167
85. Li, J., Zhao, C., Zhang, M., Yuan, F., and Chen, M. (2019). Exogenous melatonin improves seed germination in limonium bicolor under salt stress. Plant Signal. 14, 1659705. doi: 10.1080/15592324.2019.1659705
86. Castañares, J. L., and Bouzo, C. A. (2019). Effect of exogenous melatonin on seed germination and seedling growth in melon (Cucumis melo l.) under salt stress. Hortic. Plant J. 5, 79–87. doi: 10.1016/j.hpj.2019.01.002
87. Wang, K., Xing, Q., Ahammed, G. J., and Zhou, J. (2022). Functions and prospects of melatonin in plant growth, yield and quality. J. Exp. Bot. doi: 10.1093/jxb/erac233
88. Marta, B., Szafranska, K., and Posmyk, M. M. (2016). Exogenous melatonin improves antioxidant defense in cucumber seeds (Cucumis sativus l.) germinated under chilling stress. Front. Plant Sci. 7. doi: 10.3389/fpls.2016.00575
89. Sun, C., Liu, L., Wang, L., Li, B., Jin, C., and Lin, X. (2021). Melatonin: A master regulator of plant development and stress responses. J. Integr. Plant Biol. 63, 126–145. doi: 10.1111/jipb.12993
90. Wang, Y., Reiter, R. J., and Chan, Z. (2018). Phytomelatonin: A universal abiotic stress regulator. J. Exp. Bot. 69, 963–974. doi: 10.1093/jxb/erx473
91. Jahan, M. S., Shu, S., Wang, Y., Chen, Z., He, M., Tao, M., et al. (2019). Melatonin alleviates heat-induced damage of tomato seedlings by balancing redox homeostasis and modulating polyamine and nitric oxide biosynthesis. BMC Plant Biol. 19, 1–16. doi: 10.1186/s12870-019-1992-7
92. Shi, H., Reiter, R. J., Tan, D. X., and Chan, Z. (2015a). Indole-3-acetic acid inducible 17 positively modulates natural leaf senescence through melatonin-mediated pathway in Arabidopsis. J. Pineal Res. 58, 26–33. doi: 10.1111/jpi.12188
93. Xu, W., Cai, S. Y., Zhang, Y., Wang, Y., Ahammed, G. J., Xia, X. J., et al. (2016). Melatonin enhances thermotolerance by promoting cellular protein protection in tomato plants. J. Pineal Res. 61, 457–469. doi: 10.1111/jpi.12359
94. Bhat, K. A., Mahajan, R., Pakhtoon, M. M., Urwat, U., Bashir, Z., Shah, A. A., et al. (2022). Low temperature stress tolerance: An insight into the omics approaches for legume crops. Front. Plant Sci. 13. doi: 10.3389/fpls.2022.888710
95. Wu, J., Nadeem, M., Galagedara, L., Thomas, R., and Cheema, M. (2022). Recent insights into cell responses to cold stress in plants: Signaling, defence, and potential functions of phosphatidic acid. Environ. Exp. Bot., 105068. doi: 10.1016/ j.envexpbot.2022.105068
96. Dahal, K., Kane, K., Gadapati, W., Webb, E., Savitch, L. V., Singh, J., et al. (2012). The effects of phenotypic plasticity on photosynthetic performance in winter rye, winter wheat and brassica napus. Physiol. Plant 144, 169–188. doi: 10.1111/j.1399 3054.2011.01513.x
97. Kaura, V., Malhotra, P., Mittal, A., Sanghera, G., Kaur, N., Bhardwaj, R., et al. (2022). Physiological, biochemical, and gene expression responses of sugarcane under cold, drought and salt stresses. J. Plant Growth Regul.,1–10. doi: 10.1007/s00344-022-10850-8
98. Gitelson, A. A., Gritz, Y., and Merzlyak, M. N. (2003). Relationships between leaf chlorophyll content and spectral reflectance and algorithms for non-destructive chlorophyll assessment in higher plant leaves. J. Plant Physiol. 160, 271–282. doi: 10.1078/0176-1617-00887
99. Yang, X., Ren, J., Li, J., Lin, X., Xia, X., Yan, W., et al. (2022). Meta-analysis of the effect of melatonin application on abiotic stress tolerance in plants. Plant Biotechnol. Rep.,1–14. doi: 10.1007/s11816-022-00770-0
100. Ghaderian, S. M., Ghasemi, R., Heidari, H., and Vazirifar, S. (2015). Effects of Ni on superoxide dismutase and glutathione reductase activities and thiol groups: a comparative study between alyssum hyperaccumulator and non-accumulator species. Aust. J. Bot. 63, 65–71. doi: 10.1071/BT14282
101. Nahar, K., Hasanuzzaman, M., Alam, M., and Fujita, M. (2015). Roles of exogenous glutathione in antioxidant defense system and methylglyoxal detoxification during salt stress in mung bean. Biol. Plant 59, 745–756. doi: 10.1007/s10535-015-0542-x
102. Erdal, S., Genisel, M., Turk, H., Dumlupinar, R., and Demir, Y. (2015). Modulation of alternative oxidase to enhance tolerance against cold stress of chickpea by chemical treatments. J. Plant Physiol. 175, 95–101. doi: 10.1016/j.jplph.2014.10.014
103. Kołodziejczyk, I., Dzitko, K., Szewczyk, R., and Posmyk, M. M. (2016). Exogenous melatonin improves corn (Zea mays l.) embryo proteome in seeds subjected to chilling stress. J. Plant Physiol. 193, 47–56. doi: 10.1016/j.jplph.2016.01.012
104. Posmyk, M. M., Janas, K. M., and Kontek, R. (2009). Red cabbage anthocyanin extract alleviates copper-induced cytological disturbances in plant meristematic tissue and human lymphocytes. Biometals 22, 479–490. doi: 10.1007/s10534-009-9205-8
105. Shi, H., Jiang, C., Ye, T., Tan, D.-X., Reiter, R. J., Zhang, H., et al. (2015b). Comparative physiological, metabolomic, and transcriptomic analyses reveal mechanisms of improved abiotic stress resistance in bermudagrass [Cynodon dactylon (L). pers.] by exogenous melatonin. J. Exp. Bot. 66, 681–694. doi: 10.1093/jxb/eru373
106. Khalid, M., Rehman, H. M., Ahmed, N., Nawaz, S., Saleem, F., Ahmad, S., et al. (2022). Using exogenous melatonin, glutathione, proline, and glycine betaine treatments to combat abiotic stresses in crops. Int. J. Mol. Sci. 23, 12913. doi: 10.3390/ijms232112913
107. Iqbal, R., and Khan, T. (2022). Application of exogenous melatonin in vitro and in planta: a review of its effects and mechanisms of action. Biotechnol. Lett. 1-18. doi: 10.1007/s10529-022-03270-x
108. Li, X., Tan, D. X., Jiang, D., and Liu, F. (2016a). Melatonin enhances cold tolerance in drought-primed wild-type and abscisic acid-deficient mutant barley. J. Pineal Res. 61, 328–339. doi: 10.1111/jpi.12350
109. Cao, Q., Wang, W., Akhtar, S. S., Yang, F., Kong, F., Cui, Z., et al. (2022). Exogenous foliar spray of selenium (Se) alleviates cold stress by promoting photosynthesis and antioxidant defense in waxy maize. doi: 10.21203/rs.3.rs-1719103/v1
110. Tariq, A., Ullah, I., Sardans, J., Graciano, C., Mussarat, S., Ullah, A., Pe˜ nuelas, J., 2023. Strigolactones can be a potential tool to fight environmental stresses in arid lands. Environ. Res., 115966
111. Shafqat, W., Summar, A.N., Rizwana, M., Muhammad, S.H., Muhammad, J.J., Iqrar, A.K., 2021. Climate change and citrus. In: Khan, MS, Khan, IA (Eds.), Citrus-Research, Development and Biotechnology, p. 147. Eds.
112. Khan, N., Bano, A., Rahman, M.A., Rathinasabapathi, B., Babar, M.A., 2019. UPLC- HRMS-based untargeted metabolic profiling reveals changes in chickpea (Cicer arietinum) metabolome following long-term drought stress. Plant Cell Environ. 42 (1), 115–132.
113. Bermudez, R., Artur, S., Rebecca, A.M., Peter, B.R., 2021. Short-and long-term responses of photosynthetic capacity to temperature in four boreal tree species in a free-air warming and rainfall manipulation experiment. Tree Physiol. 41 (1), 89–102
114. Chi, C., Xu, X., Wang, M., Zhang, H., Fang, P., Zhou, J., Xia, X., Shi, K., Zhou, Y., Yu, J., 2021. Strigolactones positively regulate abscisic acid-dependent heat and cold tolerance in tomato. Hortic. Res. 8.
115. Pandey, A., Sharma, M., Pandey, G.K., 2016. Emerging roles of strigolactones in plant responses to stress and development. Front. Plant Sci.
116. Khalid, M.F., Iqbal Khan, R., Jawaid, M.Z., Shafqat, W., Hussain, S., Ahmed, T., Rizwan, M., Ercisli, S., Pop, O.L., Alina Marc, R., 2022. Nanoparticles: the plant saviour under abiotic stresses. Nanomaterials 12 (21), 3915.
117. L´ opez-R´ aez, J.A., 2015. How drought and salinity affect arbuscular mycorrhizal symbiosis and strigolactone biosynthesis? Planta 243 (6), 1375–1385
118. Rivero RM, Gimeno J, Van Deynze A, Walia H, Blumwald E. Enhanced cytokinin synthesis in tobacco plants expressing PSARK: IPT prevents degradation of photosynthetic protein complexes during drought. Plant & Cell Physiology. 2010;51(11):1929-1941.
119. Li, Y.J. Zhang, J.C. Zhang, J. etal. Expression of an Arabidopsis molybdenum factor sulphurase gene in soybean enhances drought tolerance and increases yield under field conditions Plant Biotechnology Journal, 11 (2013), pp. 747-758.
120. Lu Y, Li Y, Zhang J, Xiao Y, et al. Overexpression of Arabidopsis molybdenum cofactor sulfurase gene confers drought tolerance in maize. PLoS One. 2013;8:e52126.
121. Zhang JJ, Li WJ, Zhang SN, et al. The putative auxin efflux carrier OsPIN3t is involved in drought stress response drought tolerance. The Plant Journal. 2012;72:805-816
122. Kim IJD, Baek HC, Park HJ, et al. Overexpression of Arabidopsis YUCCA6 in potato results in high-auxin developmental phenotypes and enhanced resistance to water deficit Mol. Plant. 2013;6:337-349.
123. Cai ZQ , Gao Q. Comparative physiological and biochemical mechanisms of salt tolerance five contrasting highland quinoa cultivars. BMC plant biology. 2020;20(1):1-5
124. Osakabe Y, Osakabe K, Shinozaki K, Tran LS. Response of plants to water stress. Frontiers in Plant Science. 2014;5:86
125. Shukla VK, Doyon Y, Miller JC, DeKelver RC, et al. Precise genome modification in the crop species Zea mays using zinc-finger nucleases. Nature. 2009;459(7245):437-441
126. Nekrasov V, Staskawicz B, Weigel D, Jones JD, Kamoun S. Targeted mutagenesis in the model plant Nicotiana benthamiana using Cas9 RNA-guided endonuclease. Nature Biotechnology. 2013;31(8):691-693