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REVIEW

Melatonin as a Key Factor for Regulating and Relieving Abiotic Stresses in Harmony with Phytohormones in Horticultural Plants — a Review

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Abstract

Melatonin was found in plants in the late 1990s, but its function, signaling, and interaction with other phytohormones still unclear. Melatonin research in plants has increased substantially in recent years, including reports on the impact of this putative plant hormone under biotic and abiotic stress situations. Temperature extremes, salt, drought, hypoxia or anoxia, nutrient deficiency, herbicides, UV radiation stress, and heavy metal toxicity are all important obstacles to horticulture crop production worldwide. To deal with these environmental challenges, plants have evolved complex signaling networks. Phytohormones are essential for controlling plant growth, development, and stress responses. Melatonin, a pleiotropic chemical present in a variety of species, has recently emerged as a powerful regulator of plant abiotic stress tolerance. The purpose of this review is to investigate the interplay between melatonin and phytohormones in the control of abiotic stress responses in horticultural crops. We explore the interactions of melatonin with several phytohormones under various abiotic stresses.

Keywords Draught · Extreme temperature · Heavy metal toxicity · N-acetyl-5-methoxytryptamine · Phytohormones · Salinity

1 Introduction

The growth, development, and yield (quality and quantity) of various crops are greatly influenced by abiotic stresses such as extreme temperatures (high or low temperature), drought, salinity, UV, nutrient deficiency, and heavy metal toxicity (Munns 2003; Saudy 2014; Annacondia et al. 2018; He et al. 2018; Saudy et al. 2021a, 2023a; El-Bially et al. 2022a; El-Metwally et al. 2022a; El-Yazied et al.2022; Nasser et al.2022; Shaaban et al. 2023a; Shahin et al. 2023). Similar adverse impacts on crop plants were reported under biotic stresses (Saudy 2015; Saudy and Mubarak 2015; Saudy et al. 2020a, 2021b; Abou El-Enin et al. 2023). Abiotic stress leads to an increase in free radicals within plant cells, where about 1–2% of consumed oxygen is transformed into reactive oxygen species (ROS), including singlet oxygen ($^1O_2$), superoxide radical ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), hydroxyl radical ($\bullet OH$), etc., as byproducts of aerobic metabolism, which make them highly vulnerable, dramatically disturbing plant metabolism and having negative impacts on crop productivity (Sachdev et al 2021; Abd El-Mageed et al. 2022; Hadid et al. 2023; Saudy et al. 2023b). It has been proved that these stressors affect normal plant growth and development, resulting in lower agricultural yields and lower quality (El-Metwally and Saudy 2021a; Saudy et al. 2021c, 2021d, 2022; Shabbir et al 2022; El-Bially et al. 2023). In response to these adverse environmental conditions, plants have developed sophisticated signaling networks to adapt and thrive; the regulatory network comprising enzymatic and non-enzymatic antioxidant systems tends to keep the magnitude of ROS within plant cells to a non-damaging level (Shahzad et al. 2019; Sharma et al. 2019b; Demirel et al. 2020; Sachdev et al 2021; El-Metwally et al.

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2022c). Plant growth, development, and stress responses are intricately regulated by a range of phytohormones such as auxins (Zhu et al. 2013), gibberellic acid (GA) (Khan et al. 2015), abscisic acid (ABA) (Leubner-metzger 2012), salicylic acid (SA) (Horváth et al. 2007), jasmonic acid (JA) (Hashem and El-sherif 2019), ethylene (ET) (Sharma et al. 2019a), and cytokinins (CKs) (O'Brien and Benková 2013). Plant hormones assume vital roles in orchestrating the various aspects of plant life and their adaptive responses to stress (Saudy et al. 2020b; El-Metwally et al. 2022b; El-Sayed et al. 2022; Rizk et al. 2023; Swain et al. 2023). In recent times, melatonin, a multifaceted molecule primarily recognized for its role in animal physiology, has emerged as a potent and influential regulator of abiotic stress tolerance in the realm of plant biology (Altaf et al. 2023; Pan et al. 2023; Tiwari et al. 2022).

Melatonin (N-acetyl-5-methoxytryptamine) synthesis in plants can be stimulated by a range of factors, including light, temperature fluctuations, and UV radiation (Pan et al. 2023). Melatonin was discovered first in grapes and subsequently in olive oil. The highest melatonin concentrations were found in the berry exocarp (skin) of different Italian and French wine grape cultivars grown in northwestern Italy (0.9 and 0.8 ng g^{-1}), while the lowest concentration was found in the Cabernet Franc cultivar (0.005 ng g^{-1}) (Iriti et al 2006). In human, melatonin, a natural hormone secreted by the pineal gland, plays a role in the sleep–wake cycle and is generally safe for short-term use. It may help treat sleep disorders like delayed sleep phase and insomnia and may reduce response after repeated use (Iriti et al 2006). Owing to the intensive intake of melatonin-rich diets, cardiovascular health related to human nutrition improved (Meng et al. 2017). Since melatonin reduces the oxidation of molecules associated inflammation, it has anti-inflammatory potential, thus supplying food containing distinctive amount of melatonin is beneficial for reducing the harms of free radicals (Pandi-Perumal et al. 2006; Mauriz et al. 2013). Additionally, it has been documented that melatonin has antiestrogenic potential via reducing hormone-linked cancers (Sánchez-Barceló et al. 2005). Melatonin is currently recognized as an important compound in a variety of physiological processes in plants, such as seed germination (Liu et al. 2022b), root growth (Wang et al. 2022b), stomatal control (Jensen et al. 2023), and stress responses (Pan et al. 2023). Melatonin functions as a signaling molecule, regulating the growth and development of plants as well as their reactions to environmental challenges (Altaf et al. 2021a, 2021b; Jensen et al. 2023; Tiwari et al. 2022). In the horticulture sector, where the growing of crops under a variety of environmental circumstances is crucial for sustainable agriculture, the effects of melatonin on stress tolerance have particularly attracted attention.

2 Melatonin General Mechanism of Stress Mitigation

Recently, researches have focused on elucidating the complex interactions between phytohormones and melatonin in the control of abiotic stress responses in horticultural crops (Jensen et al. 2023; Wang, et al. 2022b). Melatonin lowered the levels of reactive oxygen species (ROS) and reactive nitrogen species (RNS) (Altaf et al. 2021a, 2021b; Peng et al. 2023). Melatonin had the potential to stabilize membrane systems (Tan et al. 2023) under exposure to harmful conditions like high temperatures, salinity, drought, chilling, and heavy metal toxicity (Altaf et al. 2023; Hasan et al. 2023; Kaya et al. 2023; Korkmaz et al. 2021; Tan et al. 2023). In these situations, melatonin can directly increase antioxidant enzyme activity and indirectly promote the gene expression of stress response and antioxidative systems under stress conditions. Melatonin induces the production of antioxidant enzymes, such as CAT, POD, and SOD, which help to detoxify excess hydrogen peroxide and maintain redox homeostasis. Melatonin also induces the expression of genes related to antioxidant enzymes (Sun et al. 2021). Melatonin can reduce the harms caused by salt stress via increasing the activity of antioxidant enzymes and removing hydrogen peroxide in plants (Pan et al. 2023; Zhang et al. 2021). Nevertheless, melatonin increases the production of respiratory burst oxidase homologs (RBOH), which generate superoxide radicals ($O_2^{\bullet-}$), which in turn increase hydrogen peroxide (H_2O_2) levels (Arnao and Hernández-Ruiz 2021). Melatonin signaling activates pathways that respond to abiotic and biotic stresses, including ROS- and RNS-mediated pathways (Altaf et al. 2021a, 2021b; Peng et al. 2023). Moreover, melatonin regulates various antioxidant pathways, such as the AsA-GSH cycle in tomatoes (Xu et al. 2023). Melatonin can help plants to remove harmful levels of reactive oxygen species by regulating the hydrogen peroxide-mediated signaling pathway (Altaf et al. 2021b; Peng et al. 2023). Melatonin turns on and off genes that are involved in helping plants respond to stress. As well, melatonin turns on the genes for HSFA2, GhNHX1, GhSOS1, GhAKT1, and HSP90, which help tomato seedlings survive hot temperatures (Shen et al 2021; Jannatizadeh et al 2019). Melatonin controls the expression of many genes that are involved in making and breaking down the plant hormones IAA, GA, CK, ABA, ET, JA, SA, and BR. This suggests that melatonin may interact with these other hormones in complex ways (Arnao and Hernández-Ruiz 2021). Melatonin and IAA are similar in structure. Melatonin also turns on genes that are involved in auxin signaling and transport, which leads to the formation of new roots in tomato plants (Wen et al. 2016).

The interaction between phytohormones and melatonin has important ramifications for the creation of techniques to increase crop tolerance to abiotic challenges (Jensen et al. 2023). Understanding the principles underlying their interaction might help to develop creative and sustainable strategies to lessen the negative impacts of environmental difficulties on the growth of horticultural crops (Arnao and Hernández-Ruiz 2021; He et al. 2020; Sun et al. 2021; Wei et al. 2020).

This review investigates the regulation of abiotic stressors in horticultural crops by melatonin in conjunction with phytohormones. The possible effects of melatonin on mitigating the abiotic stresses on some horticulture crops are illustrated in Table 1. It draws attention to possible gains in crop stress resistance and output. Recent developments in the use of phytohormones and exogenous melatonin improve plant resistance to abiotic stressors, with particular emphasis on the practical implications for horticultural techniques. In addition, this brings together previous research on melatonin's relationship to phytohormones, emphasizing how it controls abiotic stressors on horticultural crops. It seeks to stimulate research and create cutting-edge approaches for resilient and sustainable agricultural production in the face of global environmental issues. The probable functions of melatonin to alleviate the stresses in plants are summarized in Fig. 1 and will be explained later in this review.

3 Melatonin Biosynthesis and Degradation in Plants

Briefly, in plants, melatonin is formed enzymatically from tryptophan (Back et al. 2016). As shown in Fig. 2, several enzymes catalyze tryptophan, tryptamine, serotonin, and 5-methoxytryptamine, and eventually, melatonin is formed. Contrariwise, melatonin could be decomposed via enzymatic and non-enzymatic fate. Plants could enzymatically stimulate the hydroxylation of melatonin, as proven by the synthesis of 2-, 4-, and 6-hydroxymelatonin (Hardeland 2015; Tan and Reiter 2020). Also, non-enzymatic degradation of melatonin occurs through hydroxylation and deoxygenation mechanisms (Tan et al. 2002). It has been documented that melatonin is non-enzymatically degraded by ROS and photolitically by UV light (Hardeland et al. 2009).

4 Melatonin Impact on Abiotic Stress

Melatonin is a plant-wide abiotic stress regulator (Pan et al. 2023; Tiwari et al. 2022). Plants are vulnerable to several environmental stresses throughout their lives. Plants have evolved several coping strategies to deal with a variety of stressful environments while preserving their survival and capacity to reproduce (Araújo et al. 2014; El-Metwally and Saudy 2021b; Zubair et al. 2022). Melatonin administered exogenously improves plant tolerance to abiotic stressors (Tiwari et al. 2022). Now, we will review how melatonin interacts with various abiotic stresses (high or low temperature, drought, salinity, UV radiation, and heavy metal toxicity) in horticultural crops.

4.1 Melatonin Impact on Extreme Temperatures

High temperatures have negative impacts on plants, such as speeding leaf senescence, creating physiological and metabolic imbalances, exacerbating plant oxidative damage, and decreasing photosynthetic efficiency (Hatfield and Prueger 2015; Hu et al. 2023). These consequences result in significantly reduced plant growth, hence poor plant yields. At high temperatures, exogenous melatonin on carnation (*Dianthus caryophyllus*) enhanced biomass, damage from oxidation, and osmotic accumulation, increased photosystem II efficiency, encouraged stomatal opening, and decreased chloroplast injury by upregulating the expression of heat tolerance genes (Hu et al. 2023). In tomato, melatonin significantly maintained photosynthetic systems under heat stress by balancing electron transfer, regulating phosphorylated and redox proteins, and adjusting antioxidant enzyme activity and ROS homeostasis (Sun et al. 2022).

Also, low-temperature stress is one of the most difficult issues with tropical plants development and growth. Low temperatures produce a variety of physiological, molecular, and metabolic changes in plants (Raza et al. 2023). One of the negative impacts of cold is that it causes cell membrane damage, resulting in reduced membrane fluidity and altered ion homeostasis in plants (Ding et al. 2017; Pan et al. 2023; Raza et al. 2023). Melatonin boosts photosynthetic carbon fixation in cold-stressed tomato plants, improves antioxidant capacity, increases expression of cold-responsive genes, increases metabolite accumulation in cold-stressed plants, and protects tomato plants from cold-induced harm (Ding et al. 2017). Postharvest exogenous melatonin treatment reduced chilling damage, weight loss rate, and was effective for retarding senescence in grape and cucumber during the storage by increasing the activity of peroxidase and catalase enzyme, thereby reducing $O_2^{\bullet-}$ and H_2O_2 rates in the tissue (Nasser et al. 2022; Liu et al. 2022a).

4.2 Melatonin Impact on Drought

Drought is a global environmental challenge, negatively impacting plant growth and agricultural productivity. It reduces membrane hydration, damages proteins, and accumulates reactive oxygen species, damaging chloroplasts and mitochondria, causing cellular degeneration (El-Metwally et al. 2021; Doklega et al. 2023; Ramadan et al. 2023a, b; Shaaban et al. 2023b). Furthermore, under low water supply, the potential of crop plants to absorb water and nutrients dramatically reduced (Saudy and El-Metwally 2019,

Table 1 Effect of melatonin application on different horticultural crops as anti-abiotic stressor

Crop	Stress type	Reported effect	Reference
Pepper	Heavy metal	Melatonin alleviates heavy metal load on pepper by lowering heavy metal buildup	Altaf et al. (2023)
Tomato	Heavy metal	Melatonin protects tomato plantlets from heavy metal stress by improving nutrient absorption, root development, photosynthesis, and antioxidant activity	Altaf et al. (2021a)
Tomato	Salinity	Melatonin protects tomato seedlings from salinity stress by promoting root development, photosynthetic, and antioxidant enzymes	Altaf et al. (2021b)
Tomato	Heavy metal	Melatonin alleviates heavy metal stress on tomato genotypes by improving root development and nutrient balance	Altaf et al. (2022a)
Tomato	Drought	Melatonin reduces tomato drought stress impact through altering plant growth, root formation, photosynthesis, and antioxidant protection system	Altaf et al. (2022b)
Tomato	Salinity	Exogenous melatonin protects tomato seedlings from salinity stress	Altaf et al. (2020)
Bean	Salinity	Melatonin protects bean from salinity stress by increasing antioxidant enzymes and photosynthetic properties	Azizi et al. (2022)
Tomato	Heavy metal	Melatonin has regulatory mechanism on tomato seed germination	Cai et al. (2022)
Tomato	Acid rain stress	Melatonin mitigates acid rain stress in tomato via modulating transcriptional factors and secondary metabolite gene expression	Debnath et al. (2020)
Potato	Drought	Melatonin reduces drought stress in potato plants through influencing osmolytes, sugar metabolism, ABA balance, and antioxidant enzymes	El-Yazied et al. (2022)
Chinese cabbage	Heavy metal	Melatonin reduces cadmium toxicity in Chinese cabbage seedlings by decreasing nitric oxide buildup and IRT1 expression	Wang et al. (2021b)
Strawberry	Salinity	Melatonin foliar applications improve strawberry fruit output and quality by increasing tolerance to salinity stress	Zahedi et al. (2020)
Cucumber	Salinity	Melatonin increases seed germination in cucumber through modulating antioxidant systems, ABA and GA interaction	Zhang et al. (2014)
Cucumber	Low temperature	Melatonin promotes seed germination in cucumber via regulating ABA signaling under low Temperature stress	Zhang et al. (2022)
Tomato	Heat	Melatonin pretreatment improves heat tolerance and reduces heat-induced senescence in tomatoes by modulating ABA and GA-mediated pathways	Jahan et al. (2021)
Tomato	Heat and drought stress	Exogenous melatonin alters stomatal regulation in tomato seedlings susceptible to heat and drought stress through mechanisms other than ABA signaling	Jensen et al. (2023)
Pepper	Drought	Melatonin improves pepper plant drought tolerance by upregulating nitrogen metabolism	Kaya et al. (2023)
Pepper	Chilling stress	Melatonin improve pepper chilling stress tolerance	Korkmaz et al. (2021)
Melon	Cold	Long-distance transfer of melatonin produces cold tolerance in distant organs of melon	Li et al. (2017)
Tomato	Heat	Melatonin decrease photosynthesis oxidative damage in tomatoes under heat stress	Sun et al. (2022)
Cucumbers	Cold	Exogenous melatonin has potential in cold stress reduction in postharvest cucumbers	Liu et al. (2022a)
Grape	Drought	Exogenous melatonin's beneficial effects on grape cuttings under drought stress via enhancing antioxidant metabolites, leaf architecture, and chloroplast morphology	Meng et al. (2014)
Grape	Cold	Exogenous melatonin treatment improves quality and maintains bioactive compounds during refrigerated storage of grape berry	Nasser et al. (2022)
Blueberries	Cold	Melatonin improves blueberry fruit postharvest disease resistance by modulating the jasmonic acid signaling pathway and phenylpropanoid metabolites	Qu et al. (2022)
Apple	Cold	Melatonin promotes apple postharvest ripening by increasing gene expression of ethylene production enzymes	Verde et al. (2023)
Loquat	Drought	Physiological and transcriptional investigations demonstrate melatonin's regulatory mechanism in promoting drought tolerance in loquat	Wang et al. (2021a)
Apple	Drought	Melatonin exogenously applied for a long time prevents drought-induced leaf senescence in apple	Wang et al. (2013)

Table 1 (continued)

Crop	Stress type	Reported effect	Reference
Malus	Drought	Melatonin regulates ABA metabolism, free radical scavenging, and stomatal behavior in two malus species exposed to drought stress	Li et al. (2015)
Kiwi	Drought	Melatonin reduces drought stress in kiwifruit seedlings through promoting non-enzymatic and enzymatic antioxidative systems	Xia et al. (2020)
Peach	Cold	Melatonin therapy prevents postharvest senescence and controls the metabolism of reactive oxygen species in peach fruit	Gao et al. (2016)
Carnation	Heat	Exogenous melatonin protects carnations from heat damage by modulating growth, photosynthetic efficiency, and leaf ultrastructure	Hu et al. (2023)
Limonium bicolor	Salinity	Under salinity stress, exogenous melatonin increases seed germination	Li et al. (2019b)
Elymus nutans	Cold	Exogenous melatonin improves cold tolerance via ABA-dependent and ABA-independent mechanisms	Fu et al. (2016)

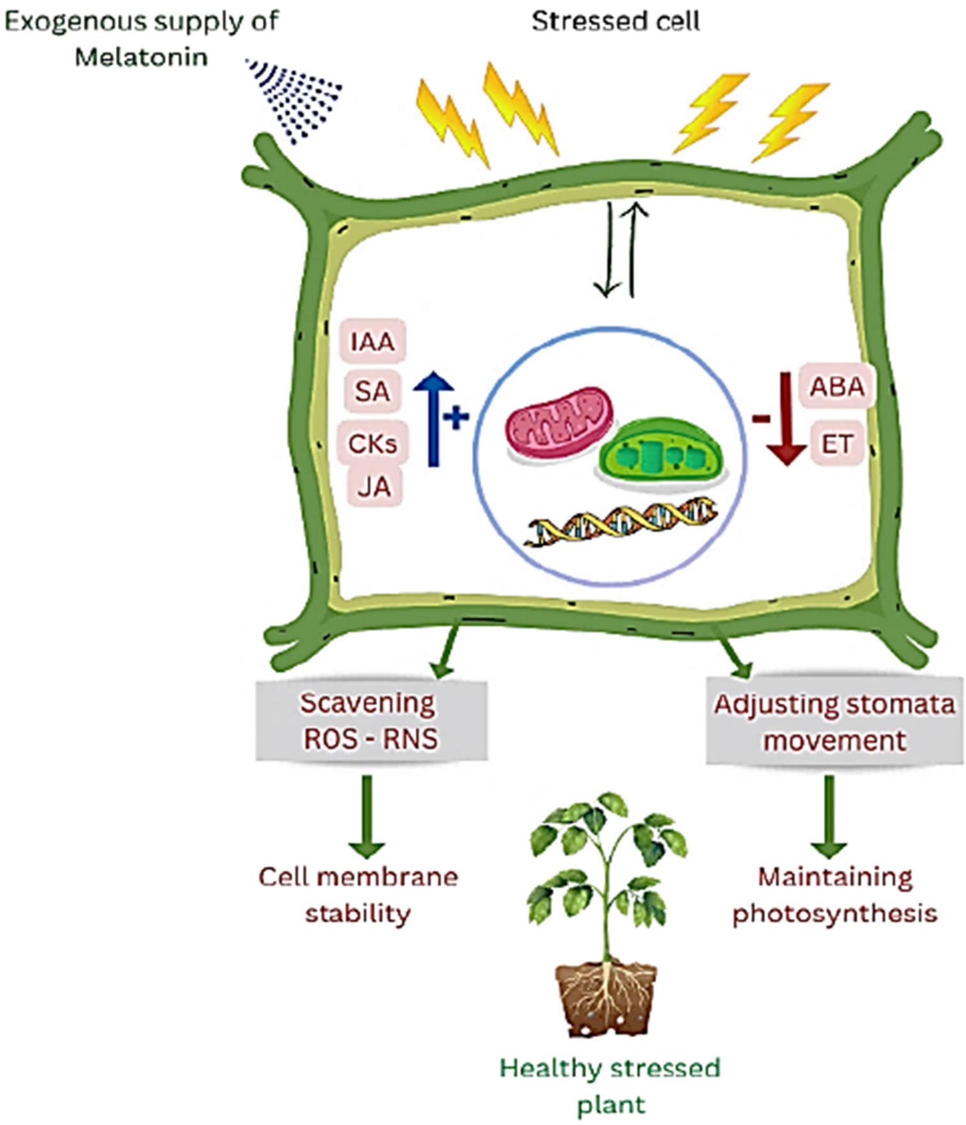

Fig. 1 Probable functions of melatonin to alleviate the stresses in plants. IAA, indole acetic acid; SA, salicylic; CKs, cytokinins; JA, jasmonic acid; ABA, abscisic acid; ET, ethylene; ROS, reactive oxygen species; RNS, reactive nitrogen species

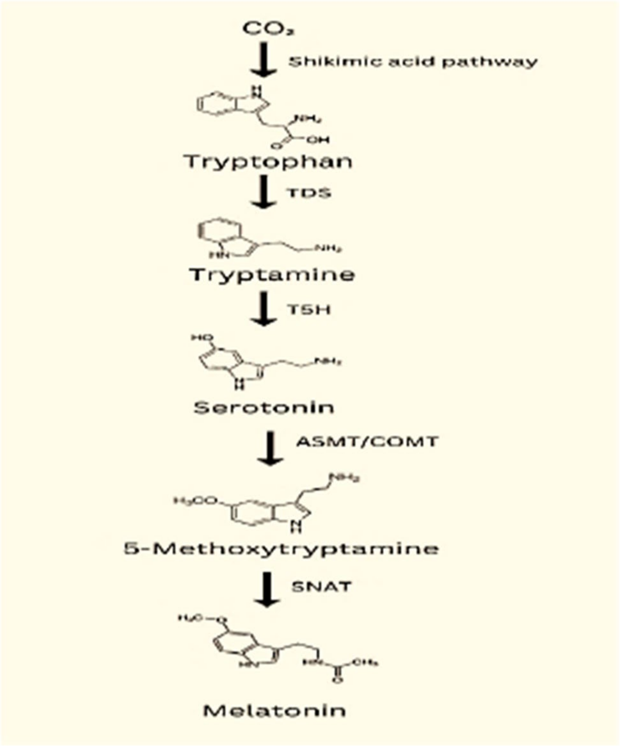

Fig. 2 Summarized explanation illustrates biosynthesis of melatonin in plants. CO_2, carbon dioxide; TDC, tryptophan decarboxylase; T5H, tryptamine 5-hydroxylase; SNAT, serotonin N-acetyltransferase; ASMT, *N*-acetylserotonin methyltransferase; COMT; caffeic acid *O*-methyltransferase

2023; Makhlouf et al. 2022). Accordingly, drought could generate nutrient deficiency (Salem et al. 2022) which dramatically injures plant growth (Noureldin et al. 2013; Saudy et al. 2018, 2020c; Ali et al. 2023). Therefore, deficit water significantly decreased yield and quality (El-Bially et al. 2018; Abd–Elrahman et al. 2022; El-Bially et al. 2022b). Melatonin lessens drought stress in kiwifruit seedlings (Xia et al. 2020). Treatment of melatonin to wine grapes leads to reducing drought stress (Meng et al. 2014). Melatonin pretreatment improved seedling development, root properties, leaf photosynthesis, and antioxidant activity, enhancing tomato seedling adaptation to drought stress (Altaf et al. 2022b).

4.3 Melatonin Impact on Salinity

Salinity is a soil condition characterized by a high concentration of soluble salts such as NaCl, the soil's most abundant and soluble salt (Munns and Tester 2008). Salinity stress has a negative influence on agricultural productivity all over the world, with a bigger impact in arid and semi-arid regions (Shahid et al. 2018). Salinity produces ionic imbalance both outside and inside the plant. First, soil salinity lowers soil water potential, resulting in a fall in water level in plants, and hence decreases in cell division, plant development, and productivity (Mubarak et al. 2021; Salem et al. 2021; Lasheen et al. 2023). The high concentration of Cl^- and Na^+ ions inside the cells, along with a low K^+/Na^+ ratio, impairs plant enzyme and membrane function, which induces cell dryness, stomata closing, and a reduction in CO_2 levels inside the photosynthetic cell (Gupta and Huang 2014; Munns and Tester 2008). Melatonin improves salinity stress–induced damage to snap bean plants by increasing proline, sugar content, and enhancing antioxidant enzyme activity (Azizi et al. 2022). Melatonin pretreatment enhanced salinity tolerance of tomato seedlings (Altaf et al. 2020). Strawberry fruit production and quality were lowered by salinity stress. Foliar melatonin reduced fruit output and quality while increasing leaf antioxidant systems and abscisic acid levels induced by salt (Zahedi et al. 2020).

4.4 Melatonin Impact on UV

Ultraviolet radiation is a part of the nonionizing radiation area of the electromagnetic spectrum and accounts for approximately 9% of solar radiation. As reported by Aboul Fotouh et al. (2014), UV is classified into three categories, i.e. UV-C (200–280 nm), UV-B (280–315 nm), and UV-A (315–400 nm). High-intensity UV exposure causes stress, suppressing photosystem II, electron transport, photosynthesis, and affecting biomass accumulation, partitioning as well as cell development, abnormal growth, and yield loss in plants (Wei et al. 2019). In apples, melatonin treatment reduced plant growth and biomass output, hindered root system development, and eased the inhibitory effects of UV-B radiation on photosynthetic systems, which reduced chlorophyll levels, stomatal apertures, and leaf membrane damage (Wei et al. 2019).

4.5 Melatonin Impact on Heavy Metal Toxicity

Heavy metals like cadmium (Cd), chromium (Cr), nickel (Ni), and vanadium (V) in growth medium disrupt key physiological processes, negatively affecting plants' life cycle from germination to production. Higher concentrations of heavy metal hinder nutrient absorption and transport, disrupting metabolic processes and affecting growth, development, and yield (Ghori et al. 2019). Melatonin boosted seedling development and leaf photosynthesis, inhibited heavy metal transfer from root to shoot, adjusted root architecture and mineral intake in pepper seedlings, and decreased oxidative damage by modulating antioxidant enzymes under heavy metal toxicity (Altaf et al. 2023). Cd-induced phytotoxicity in tomato was reduced by increasing biomass production, root system, and macro and micronutrient intake while lowering Cd uptake in tomato due to melatonin supply

(Altaf et al. 2022a). Exogenous melatonin reduces Cd toxicity in Chinese cabbage (Wang et al. 2021b).

5 Crosstalk Between Melatonin and Phytohormones

Researchers have described the interactions of melatonin with other phytohormones. Because of their chemical similarities, auxin (IAA) was the primary focus of research on the interaction of melatonin and other plant hormones (Arnao and Hernández-Ruiz 2018; Yang et al. 2021). Numerous investigations, however, have discovered fascinating links between melatonin and almost all known plant hormones, including JA, SA, brassinosteroids, polyamines, strigolactones, plant peptide hormones, and nitric oxide, gibberellin, cytokinins, ethylene, and ABA (Arnao and Hernández-Ruiz 2018; Murch and Erland 2021; Yang et al. 2021, 2022a; Wang et al. 2022c; El-Beltagi et al. 2023). By surveying the relationship between melatonin and various plant hormones, which will be explained later in this article, we can illustrate their possible interactions in Fig. 3.

5.1 Melatonin and Auxin Crosstalk

IAA is the primary auxin in plants, controlling growth and development processes such as cell division and elongation, tissue differentiation, apical dominance, and responses to light, gravity, and pathogens (Fu et al. 2015). Melatonin stimulates growth in the same manner as auxin and indolyl-3-acetic acid (IAA) do (Hernández-Ruiz et al. 2004; Arnao and Hernández-Ruiz 2006).

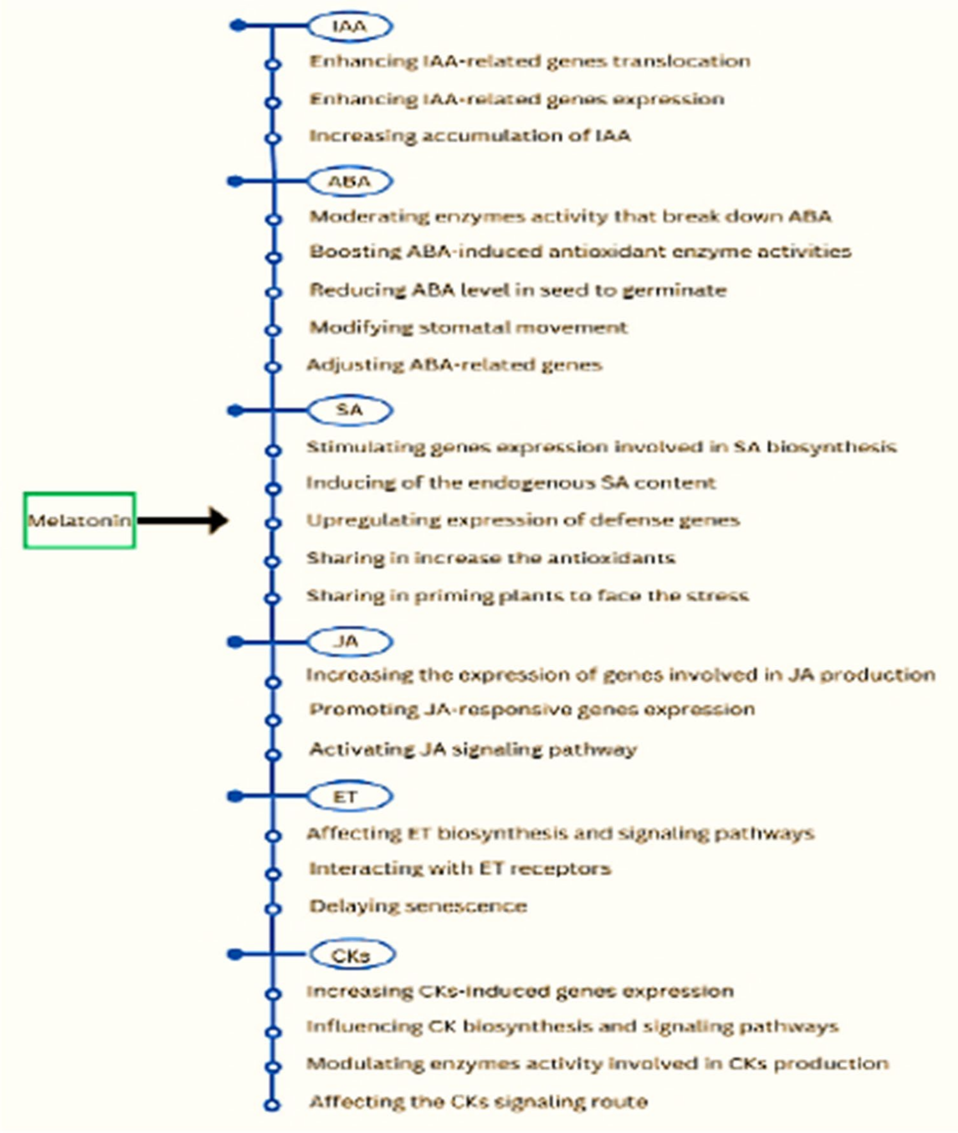

Fig. 3 The interference between melatonin and various phytohormones in stressed plants. IAA, indole acetic acid; SA, salicylic; CKs, cytokinins; acid; JA, jasmonic acid; ABA, abscisic acid; ET, ethylene; ROS, reactive oxygen species; RNS, reactive nitrogen species

Regarding the regulation of auxin biosynthesis and metabolism, both melatonin and auxin have the same precursor, tryptophan, and can be converted into IAA or IAA agonists. Melatonin, when applied exogenously, promotes root development in a manner similar to IAA (Wen et al. 2016). Melatonin therapy increases mustard and tomato seedling development and influences IAA and IBA biosynthesis. Melatonin treatment at 50 M has been demonstrated to increase the expression of auxin signal-transduction genes (*IAA19 and IAA24*) as well as auxin efflux genes (*PIN1*, *PIN3*, and *PIN7*), which promote the formation of adventitious roots in tomato (Chen et al. 2009; Wen et al. 2016). On the other hand, melatonin treatment at 600 M reduces auxin production levels and transport routes, as demonstrated by lower expression of *YUC1*, *YUC2*, *YUC5*, *YUC6*, *TAA1*, *TAR2*, *PIN1*, *PIN3*, and *PIN7*. Melatonin at concentrations ranging from 10 to 20 mM increases the expression of *Os01g08320* (*OsIAA1*), *Os02g56120* (*OsIAA9*), *Os02g57250* (*OsIAA10*), *Os06g07040* (*OsIAA20*), and *Os011g11410* (*OsIAA27*) (Chen et al. 2009; Wen et al. 2016). These data imply that melatonin mimics IAA in plants at low doses (Chen et al. 2009; Wen et al. 2016).

To see if there was an interaction between melatonin and IAA, researchers looked at the expression of genes involved in IAA production and signal transduction. Melatonin increased the expression of *MdYUCCA1*, *MdYUCCA10*, *MdARF7*, and *MdARF19*. Melatonin also increased the expression of the IAA transport-related genes *MdAUX1*, *MdPIN1*, and *MdPIN3* (Mao et al. 2020). Concerning the relation between IAA and melatonin in mitigating the stresses, exogenous IAA addition can reduce the toxic effect of Cd in *Cinnamomum camphora* leaves via increasing total chlorophyll and carotenoid content; decreasing proline, soluble sugar, and MDA content; and improving photosynthetic performance (Zhou et al. 2020). Exogenous IAA could lessen Cd adverse effects in tea via reduction its accumulation (Zhang et al. 2020). Mitigation of copper toxicity in germinating seeds of pea using IAA was observed (Ben Massoud et al. 2017). Using IAA boosted yield of broad beans in high salinity conditions (Latef et al. 2021). In this connection, melatonin treatment raised the accumulation of IAA and crosstalk happened between melatonin and IAA during adventitious root formation in apple (Mao et al. 2020). Melatonin could alleviate cold tolerance via IAA accumulation in watermelon (Li et al. 2017).

5.2 Melatonin and ABA Crosstalk

ABA is a vital phytohormone involved in several physiological processes, such as stomatal closure, reacting to stress, and seed dormancy (Liao et al. 2023; Ortiz-García et al. 2023; Seo and Koshiba 2002). In addition, ABA is known as the "universal stress hormone" because it simultaneously regulates plant growth and development and governs the production of a number of defensive metabolites that help plants fight off the negative effects of stressful environments (Singh et al. 2022). ABA played critical role in plants' ability to mitigate the detrimental effects of abiotic stress through the regulation of gene expression, stomatal closure, production of protective metabolites, and other adaptive biochemical processes (Parwez et al. 2022). Plant responses to abiotic stressors are modulated by melatonin's effects on ABA levels and signaling pathways. The crosstalk between melatonin and ABA plays a meaningful position in the regulation of abiotic stress responses in horticulture crops (Jensen et al. 2023). Here, we go through the workings of melatonin-ABA crosstalk in horticultural crops.

Exogenous melatonin treatment reinforces the expression of key ABA biosynthesis genes like 9-cis-epoxycarotenoid dioxygenase (Banerjee and Roychoudhury 2019; Fu et al. 2016; Singh et al. 2022). According to prior research, endogenous melatonin production and the expression of the EnCOR14a and EnCBFs genes were both dramatically elevated in response to cold stress (Fu et al. 2016). This shows that both ABA-dependent and ABA-independent mechanisms are involved in melatonin's ability to promote cold tolerance (Fu et al. 2016). Melatonin can also control ABA metabolism by moderating the activity of enzymes that break down ABA, including ABA 8′-hydroxylase in watermelon (Li et al. 2020). The total ABA levels in plants are influenced by melatonin's control of ABA production and metabolism.

Each of melatonin and ABA has the potential to control ROS scavenging and antioxidant defense mechanisms (Fu et al. 2016). ABA stimulates the genes that produce antioxidant enzymes, which improves the detoxification of ROS. There is evidence that the signal molecule of ABA can cause the expression of genes, start a signal transduction pathway, and prepare plants to respond to stress (Fujita et al. 2011; Nakashima et al. 2006; Xu et al. 2022). According to earlier research on pea, ABA enhanced the amount of ROS and the activity of antioxidant enzymes against oxidative stress, and calcium dioxide and ROS crosstalk is crucial to the ABA-induced antioxidant defense (Xiong et al. 2006). Like other powerful antioxidants, melatonin may directly scavenge ROS (Li et al. 2015). Melatonin can boost ABA-induced antioxidant enzyme activities, lower ROS levels, and lessen oxidative stress in horticultural crops that have been subjected to abiotic stressors, according to studies in apple (He et al. 2020; Li et al. 2020), cassava (Wei et al. 2020), pepper (Altaf et al. 2023; Kaya et al. 2023), tomato (Hasan et al. 2023; Peng et al. 2023), cucumber (Zhang et al. 2014), and strawberry (Hayat et al. 2022).

Under adverse circumstances, ABA prevents germination and encourages seed dormancy maintenance (Fujita et al. 2011). Melatonin could influence ABA-mediated seed germination and dormancy (Zhang et al. 2014). Melatonin controls seed germination by favorably upregulating ABA catabolism and GA biosynthesis. To the best of our knowledge, the cucumber research explains how melatonin reduces the inhibitory effect of salt stress on cucumber germination (Zhang et al. 2014). According to some reports, melatonin therapy can induce seed dormancy by lowering ABA concentrations and changing the expression of genes that respond to ABA (Zhang et al. 2022, 2014). Under salt stress, melatonin down-regulated ABA biosynthesis genes (*e.g., CsNECD2*) in cucumber (Zhang et al. 2014). Melatonin-treated seeds had high levels GA, low levels of ABA, and high levels of amylase and alpha-amylase activity during germination. The ABA 8-hydroxylase genes (*LbCYP707A1* and *LbCYP707A2*), which mediate the changes in GA and ABA levels in seeds during germination, were upregulated by melatonin treatment, as were key genes involved in GA biosynthesis (*GA20ox and GA3ox*). Key genes involved in ABA *biosynthesis* (*LbNCED1 and LbNCED3*) were downregulated by melatonin treatment. Melatonin in seeds encourages food uptake and protein synthesis to speed up seed germination in sea-lavender (Li et al. 2019b). Under stress, melatonin and ABA's interplay in seed dormancy control aids in the effective germination and establishment of horticultural crops such as cucumber (Zhang et al. 2022), sea-lavender (Li et al. 2019b), tomato (Cai et al. 2022), and almond (García-Sánchez et al. 2022).

Stomatal closure is a crucial adaptive response of plants to reduce water loss under abiotic stress conditions. Melatonin and ABA interact to control stomatal movements (Li et al. 2015; Yang et al. 2022b). Previous studies pointed out that melatonin may contribute in stomatal movement by regulating the ABA (Yang et al. 2022b). Another work presented that melatonin be capable of control stomatal movement in response to stress through interacting with the phytohormone ABA (Wang et al. 2023). Melatonin encouraged stoma closure by regulating the K^+ channel (Wang et al. 2023). Under stressful circumstances, melatonin-ABA interaction leads to increased water usage effectiveness and decreased water loss (Li et al. 2020; Yang et al. 2022a).

Melatonin and ABA act together in the adjustment of stress-responsive genes implicated in abiotic stress tolerance. Stress-related genes, such as those that code for the late embryogenesis abundant proteins in watermelon (Li et al. 2019a), osmo-protectants in tomato (Mushtaq et al. 2022), and stress-responsive transcription factors can be induced by both melatonin and ABA (Alam et al. 2018; Wang et al. 2021b). Melatonin has been found to increase ABA-induced gene expression, which improves ABA-induced stress tolerance in horticultural crops such as in grape (Xu et al. 2018) and tomato (Jahan et al. 2021).

5.3 Melatonin and SA Crosstalk

Since SA is involved in both plant immunity and defense mechanisms against pathogens and abiotic stressors (Nejat and Mantri 2017; Prakash et al. 2021). On the other hand, melatonin has been proven to be a powerful antioxidant and a regulator of plant stress responses (Pan et al. 2023; Tiwari et al. 2022). An essential component of plant defense mechanisms and stress tolerance in horticultural crops is the interaction between the melatonin and SA.

Melatonin can affect signaling and SA biosynthesis pathways (Esmaeili et al. 2023). Studies have revealed that melatonin can increase the expression of crucial genes involved in SA biosynthesis, such as isochorismate synthase and phenylalanine ammonia-lyase (Pérez-Llorca et al. 2019). Chorismate can be changed into isochorismate, and that compound can then be changed into SA when isochorismate synthase is activated by melatonin (Pérez-Llorca et al. 2019). In kiwi, due to the upregulation of the expression of SA-responsive phenylalanine ammonia-lyase (PAL), melatonin pretreatment enhanced endogenous SA production primarily via the PAL pathway, activating the kiwifruit defensive response to chilling stress (Guo et al. 2023). In another study on peach, melatonin pretreatment stimulated PAL activity, which in turn increased endogenous SA content, helping to counterbalance the ratio of unsaturated to saturated fatty acids in peach fruit and reducing membrane lipid peroxidation (Guo et al. 2023). Cherry tomato fruit may be more resistant to *Botrytis cinerea* infection via exogenous melatonin. Disease resistance to *Botrytis cinerea* caused by melatonin is reliant on SA buildup and the SA signaling system (Li et al. 2022). Melatonin can also modify SA signaling by influencing the expression of genes that are SA sensitive and interacting with SA receptors (Guo et al. 2023).

Melatonin and SA are capable to induce the expression of defense-related genes implicated in plant immunity(Guo et al. 2023; Li et al. 2022; Nejat and Mantri 2017). Melatonin has been demonstrated to increase the expression of genes producing pathogenesis-related (PR) proteins, which are important in plant defense against pathogens (Guo et al. 2022; Li et al. 2022). Melatonin treatment significantly inhibited gray mold development, induced ROS burst, increased SA accumulation accompanied by increased activity of its synthesis-related enzymes, upregulated expression of defense genes like *SlWRKY70*, *SlTGA5*, *SlPR1*, *SlPR2*, *SlNPR1*, and *SlGLU*, but decreased nitric oxide (NO) content during storage in cherry tomato. Furthermore, melatonin therapy boosted endogenous melatonin concentration in fruit during storage by upregulating the expressions of *SlTDC*, *SlSNAT*, and *SlASMT* (Li et al. 2022). The interaction between melatonin and SA results in a synergistic influence on the activation of defense-related genes, indicating increased resistance of horticulture plants against biotic and abiotic stresses.

Melatonin and SA are regarded as antioxidants that can affect the efficacy of plant antioxidant defense systems (Pieterse and Van Loon 1999; Yang et al. 2022b). Both compounds can scavenge ROS and reduce oxidative stress (Horváth et al. 2007; Pan et al. 2023). Melatonin has been demonstrated to boost the activity of antioxidant enzymes including superoxide dismutase (SOD) and catalase (CAT), as well as the accumulation of non-enzymatic antioxidants like glutathione and ascorbate. Melatonin caused a burst of ROS, elevated endogenous melatonin and SA, and boosted chitinase (CHI) and 1,3-glucanase (GLU) activity in tomatoes. Furthermore, the treatment altered the phenylpropanoid pathway by boosting the activities of PAL, 4-coumarate-coenzyme A ligase (4CL), and peroxidase (POD) in tomato, which was followed by greater levels of lignin, flavonoids, and total phenols (Li et al. 2019c). Melatonin-treated tomato seedlings show improved pigment content, antioxidant enzyme activity, and reduced malondialdehyde (MDA) levels (Debnath et al. 2020). To scavenge ROS and prevent membrane peroxidation, the antioxidant enzymes SOD, POD, CAT, APX, and GR are required. The activity of these enzymes increased when supplemented with single and combination melatonin and *Trichoderma* treatments in a pak choi research. Furthermore, the use of melatonin and *Trichoderma* inhibits the production of H_2O_2 in roots, which is consistent with an increase in CAT activity. The treatment of melatonin and *Trichoderma* controls pak choi clubroot disease by enhancing enzymatic activities (Gulzar et al. 2023). Melatonin increases the contents of ascorbic acid (AsA) and glutathione (GSH) in tomato (Xu et al. 2023). SA also stimulates the production of antioxidant enzymes and increases plant antioxidant capacity (Horváth et al. 2007; Pieterse and Van Loon 1999; Srivastava and Dwivedi 1998). SA application increased the content of SOD, CAT, APX, AsA, GSH, and DPPH scavenging capacity, but inhibited the accumulation of ROS and MDA in longans (Zhang et al. 2023). Thus, melatonin and SA interaction in regulating antioxidant defense systems influences the mitigation of oxidative injury in stress conditions.

Priming is the process by which plants are prepared to generate a quicker and stronger defensive response in the event of future stress exposure (Rakshit and Singh 2018). Melatonin and SA treatments are able to prime plants, resulting in greater defensive response and stress tolerance (Alam et al. 2022; Rajora et al. 2022). Seed priming with SA showed better performance, especially to severe soil moisture-deficit conditions. This is due to SA's external supplementation maintaining high chlorophyll content (SPAD value), membrane stability index, osmotic potential, and reducing electrolyte leakage in cantaloupe (Alam et al. 2022). Melatonin priming (5, 10, 25 uM) was administered to leek seeds, and germination was examined at optimal (21 °C), chilling stress (7 °C), and high temperature (35 °C). Treatment with 5 M melatonin increased seedling resistance and germination in chilling stress (Jannatizadeh et al. 2019). The findings from the sweet corn study suggested that melatonin priming might increase sweet corn tolerance to oxidative stress by increasing antioxidant enzyme activity and decreasing herbicide harm (Fathi et al. 2023).

5.4 Melatonin and JA Crosstalk

Melatonin-jasmonic acid (JA) interaction is an important component of plant defense and stress responses in horticultural plants. JA is an important phytohormone that plays a role in a variety of physiological processes, including plant growth, development, and defense against biotic stressors (Wang et al. 2020a). The mechanisms and consequences of melatonin-JA crosstalk in the modulation of abiotic stressors in horticultural crops are discussed here.

A study on litchi fruit supports the effect of melatonin on jasmonic acid. Melatonin therapy has been demonstrated in studies to increase the expression of essential genes involved in JA production, like lipoxygenases (LOX) in litchi fruit (Wang et al. 2020b) and allene oxide synthase (AOS) in blueberries (Qu et al. 2022). Adjustment of JA biosynthesis and metabolism via melatonin contributes to the activation of defense responses against abiotic stresses. JA plays as a signaling molecule through binding to its receptor, coronatine-insensitive protein 1 (COI1), indicating to degradation of JASMONATE ZIM-domain (JAZ) repressor proteins and successive activation of JA-responsive genes (Abdelkareem et al. 2017; Ishiga et al. 2013; Wang et al. 2020a). Melatonin therapy has been demonstrated to increase the expression of JA-responsive genes, indicating a function in JA signaling control (Qu et al. 2022; Wang et al. 2020a). This connection between the melatonin and JA signaling pathways helps to activate stress-responsive genes implicated in abiotic stress tolerance.

Both melatonin and JA play important roles in plant defense against biotic stressors (Pan et al. 2023; Wang et al. 2020a). Melatonin has been found to improve plant tolerance to diseases and pests (Pan et al. 2023; Qu et al. 2022). In a similar manner, JA participates in the regulation of defense-related genes as well as the generation of secondary metabolites like phytoalexins and volatile organic compounds (VOCs), which aid in plant defense against herbivores and pathogens (Gols et al. 1999; Okada et al. 2015). The crosstalk of melatonin with JA has a synergistic impact on the activation of defensive mechanisms, resulting in increased plant tolerance to both biotic and abiotic stressors. Melatonin and JA could scavenge ROS and reduce oxidative stress. Melatonin treatment improves antioxidant enzyme activity and increases non-enzymatic antioxidant accumulation (Gulzar et al. 2023; Xu et al. 2023). As well, JA is involved in the regulation of antioxidant defense mechanisms (Okada et al. 2015). Tomato responses to *Bemisia tabaci* nymphs are mediated by JA signaling (Zhang et al. 2018). In guava, JA decreases chilling injury and stimulates fruit defense reaction as signaled by the behavior of total phenols and boost in sugar content, lipoxygenase (LOX) and phenylalanine-ammonia lyase (PAL) activities (González-Aguilar et al. 2004). In tomato, the pretreatment of tomato fruit with JA increases the synthesis of some stress proteins, like PR proteins, which leads to improved chilling tolerance and disease resistance, lessening the incidence of decay (Ding et al. 2002). Melatonin encourages disease tomato fruit resistant to *Botrytis cinerea* by activation the JA signaling pathway (Liu et al. 2019). Melatonin and JA boost antioxidant capacity, which reduces cold-induced oxidative damage in watermelon (Guo et al. 2021). Melatonin and JA's interplay in altering antioxidant defense systems adds an extra layer of protection against oxidative damage under abiotic stress situations.

5.5 Melatonin and ET Crosstalk

Melatonin and ethylene (ET) had an important role in plant stress reactions and growth regulation in horticulture plants (Chen et al. 2021; Pan et al. 2023). ET is an essential phytohormone implicated in several physiological routes, with seed germination, fruit ripening, senescence, and responses to biotic and abiotic stresses (Chen et al. 2021; Sharma et al. 2019a). Ripening is a coordinated array of developmental and physiological activities that create changes in color, fragrance, and nutritional content in fleshy fruits such as bananas, apples, peaches, strawberries, melons, squash, and tomatoes (Chen et al. 2023; Gambhir et al. 2023; Gupta et al. 2022; Liu et al. 2023; Verde et al. 2023; Wei et al. 2022). Ripening and senescence are quite similar; however, ripening is a separate phase for fleshy fruit that precedes and may predispose the fruit to senescence, according to metabolic activity. Ethylene is a gaseous phytohormone that regulates plant development and fruit ripening. Extensive research on fruit ripening triggered by ethylene through its sensing, signaling, and gene regulation processes has investigated the role of ethylene in fruit ripening, which has been observed in fruit crops (Gupta et al. 2022).

Melatonin has the ability to affect ET biosynthesis and signaling pathways (Verde et al. 2023). ET is produced from methionine via enzymatic processes, with 1-aminocyclopropane-1-carboxylic acid (ACC) serving as an intermediary (Fatma et al. 2022; Gupta et al. 2022). Melatonin has been demonstrated to influence the activity of the major enzymes in ET production, ACC synthase (ACS) and ACC oxidase (ACO) (Wang et al. 2022a). In pak choi study, melatonin also significantly maintained chlorophyll concentration by limiting ethylene formation and action throughout shelf life, which is most likely due to decreased activities of 1-aminocyclopropane-1-carboxylate (ACC) synthase (ACS) and ACC oxidase (ACO), as well as expression levels of their associated genes (Wang et al. 2022a). Melatonin reduced postharvest pak choi leaf yellowing due to regulation of ethylene production and respiratory metabolism (Wang et al. 2022a). Furthermore, melatonin can also influence ET signaling by influencing the expression of ET-responsive genes and interacting with ET receptors in tomato (Yang et al. 2022a). Melatonin regulates ET production and transduction, which helps to modulate plant stress responses.

ET is well known for its function in plant development and growth, including cell elongation, leaf senescence, and fruit ripening (Gambhir et al. 2023). Melatonin has been linked to the control of these processes (Verde et al. 2023; Wang et al. 2022a; Yang et al. 2022b). Melatonin has been demonstrated in studies to impact ET-induced cell elongation and modulate the functioning of genes associated with leaf senescence and fruit ripening (Ahmad et al. 2023; Wang et al. 2022a). Melatonin and ET interact to regulate development and growth functions, which helps to fine-tune plant responses to environmental stimuli.

ET is known to influence leaf senescence, a closely regulated process that involves the intentional destruction of cellular components (Koyama 2014). Melatonin has been investigated to delay senescence in a variety of horticulture plant types (Zhao et al. 2021). In apples, melatonin consumption was connected to a considerable delay in drought-induced leaf senescence. This delayed the drought-related decreases in PSII photosynthesis and photochemistry efficiency. Melatonin's regulatory role has a significant anti-senescence impact, in detached leaves (Wang et al. 2013). In peach, melatonin treatment delayed senescence and preserved peach fruit quality, decreased ROS generation and blocked membrane lipid peroxidation, promoted antioxidant enzyme activity, and reduced oxidative stress (Gao et al. 2016). In pears, mmelatonin inhibited, rather than increased, ethylene bursts during pear fruit senescence, as well as protected mature pear fruit from experiencing physiological problems and may also help to preserve the commercial worth of pear fruit (Zhai et al. 2018).

Melatonin and ET play key responsibilities in plant stress responses and tolerance (Ahmad et al. 2023; Chen et al. 2021). ET influences the regulation of stress-responsive genes as well as the antioxidant defense mechanisms (Chen et al. 2021). The antagonistic interactions between several components of the ABA and JA-ET signaling pathways alter defense- and stress-responsive gene expression in response to biotic and abiotic stimuli (Anderson et al. 2004). ET governs physiological, developmental, and reaction to stress by activating ET response Factors (ERFs), which are members of a vast multigene family of transcription factors. ERF genes are important regulators of abiotic stress responses and may be suitable for tomato stress resistance (Klay et al. 2018). Melatonin and ET interact, resulting in a synergistic impact on stress tolerance (Wang et al. 2022a). Ethylene could contribute to effective melatonin alleviation of Cd toxicity in radish roots (Xu et al. 2023).

5.6 Melatonin and CKs Crosstalk

CKs are important phytohormones that govern cell division, shoot growth, root formation, and other physiological activities (O'Brien and Benková 2013; Hassan et al. 2018; Saidi and Hajibarat 2021; Tawfik et al. 2022). Melatonin has been demonstrated in studies to alter CKs (Abd El-Naby et al. 2019; Arnao and Hernández-Ruiz 2021; Zhang et al. 2017). Using melatonin enhances plant tolerance to abiotic stressors by increasing CK-induced gene expression and antioxidant enzyme activity (Abd El-Naby et al. 2019; Mao et al. 2020; Zhang et al. 2017).

Melatonin has been shown to alter plant hormonal levels, physiological activities, and gene synthesis. Melatonin could affect CK biosynthesis and signaling pathways. Through a sequence of enzymatic processes, CKs are produced from isopentenyladenine (iP) and adenosine phosphate (Márquez-López et al. 2019). Melatonin has been demonstrated to impact CK levels in plants via modulating the activity of enzymes involved in CK production, such as isopentenyl transferase (IPT) (Arnao and Hernández-Ruiz 2021). Exogenous melatonin supply raised CK levels under heat stress by upregulating LpIPT2 and LpOG1, essential CK-biosynthesis-related genes, but melatonin had little effect on CK levels in non-stress settings. Melatonin also affected the CK signaling route by modulating A-ARRs and B-ARRs, transcription factors implicated in CK signaling pathways (Zhang et al. 2017). Melatonin's control of CK biosynthesis and signaling leads to the modulation of plant growth and reactions to stress.

CKs play a vital action in promoting cell division, shoot growth, and overall plant development (Márquez-López et al. 2019; Saidi and Hajibarat 2021). CKs improve shoot growth and yield in salinized tomato (Ghanem et al. 2011). Synthetic cytokinins prolong the period of division of parenchyma cells in growing pears (Shargal et al. 2015). Melatonin has been shown to control plant growth and development, such as shoot elongation, root development, and flower induction in apricot (Abd El-Naby et al. 2019). Melatonin has been demonstrated in studies to alter CK-induced shoot elongation as well as the expression of genes involved in root development and branching (Abd El-Naby et al. 2019; Arnao and Hernández-Ruiz 2021; Zhang et al. 2017). Melatonin encourages adventitious root formation in apple (Mao et al. 2020). Melatonin appears to increase adventitious root growth in cucumber seedlings by influencing the expression of genes involved in hormone production, signaling, and cell wall construction (Wang et al. 2022c).

The interplay of melatonin and CKs in senescence control might entail the modulation of senescence-related gene expression as well as the regulation of ROS levels. In cucumber, leaf senescence increased the accumulation of endogenous melatonin by causing differential expression *of CST5H*, *CsASMT*, and *CsTDC*. The application of melatonin alleviated leaf senescence caused by darkness or age by downregulating the mRNA abundances of *SAG12* and cell death-related gene *PDCD*, improving chlorophyll content due to normal chloroplast ultrastructure and reduce mRNA abundances of chlorophyll degradation genes, upregulating stages of proteins related to the Calvin-Benson cycle and PSI and PSII reaction centers, and in the end razing photosynthetic efficiency and yield of cucumber (Liu et al. 2022a).

Together, melatonin and CKs are implicated in the regulation of stress responses in horticulture crops (O'Brien and Benková 2013; Pan et al. 2023; Shargal et al. 2015). CKs have been shown to enhance plant tolerance to abiotic stresses, such as drought and salinity (O'Brien and Benková 2013). Cytokinin converse salinity stress tolerance in *Vicia faba* (Abdel- Latef et al. 2021). In eggplant, CK may be able to mitigate the negative effects of salt stress on plant development by boosting photosynthetic efficiency and strengthening antioxidant enzyme systems in leaves (Wu et al. 2012). Regarding melatonin and CKs interaction, melatonin has been found to promote plant tolerance to abiotic stressors by increasing CK-induced stress-responsive gene expression and antioxidant enzyme activity (Abd El-Naby et al. 2019; Mao et al. 2020; Wang et al. 2022c; Zhang et al. 2017).

6 Conclusions and Future Prospects

Understanding the complex interplay between melatonin and phytohormones gives important insights into the processes underpinning abiotic stress tolerance in horticultural crops. Melatonin-phytohormone interactions govern a variety of physiological and biochemical processes involved in stress adaption, including as ROS scavenging, antioxidant defense, transcriptional regulation, stomatal regulation, and ion homeostasis. Using creative agronomic methodologies and genetic engineering technologies to harness these interactions may offer interesting possibilities for improving abiotic stress tolerance in horticultural crops, assuring sustainable crop production in tough conditions.

One of the most promising prospects for using melatonin in conjunction with plant hormones is to develop new strategies to reduce the effects of climate change. Climate change is expected to lead to increased frequency and severity of abiotic stresses, such as drought, salinity, and extreme temperatures. Melatonin and plant hormones can be used to develop new crop varieties that are more tolerant to these stresses (Nawaz et al. 2016). For example, researchers have shown that melatonin can be used to improve thermotolerance drought, and salt tolerance in some crops. Plant hormones can also be used to improve stress tolerance in crops. Herein, ABA can be used to increase stomatal closure, which can help to reduce water loss during drought. Auxin can be used to promote root growth, which can help plants to access water and nutrients during drought. Cytokinin can be used to delay senescence, which can help plants to survive longer periods of stress. By combining melatonin and plant hormones, researchers can develop new crop varieties that are highly tolerant to a variety of abiotic stresses. This will help to ensure food security in the face of climate change.

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Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of Interest The authors declare no competing interests.

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