Synergistic Effect of Melatonin in Plant Growth and Development in Stress Mitigation

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Abstract

Melatonin, known as N-acetyl-5-methoxy-tryptamine, has emerged as a fascinating hormone with multifaceted roles in plant growth, development, and stress mitigation. In recent years, its presence in plants has sparked considerable interest, prompting extensive research to unravel its diverse functions beyond the traditional understanding. This chapter presents a comprehensive exploration of the synergistic effects of melatonin on plant growth and development, with a particular focus on its remarkable potential as a stress-mitigating agent. The role of melatonin in plant growth and development is increasingly recognized, as studies reveal its involvement in various physiological processes. From seed

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germination to flowering and fruit development, melatonin appears to play a critical regulatory role in shaping plant life cycles. Additionally, its impact on root architecture, shoot elongation, and leaf morphology further supports its significance in plant growth. Melatonin's stress-mitigating properties have captured the attention of researchers and agriculturists alike. As an antioxidant, melatonin exhibits a remarkable ability to scavenge reactive oxygen species, protecting plants from oxidative stress induced by biotic and abiotic factors. This stress-mitigating effect extends to challenging environmental conditions such as extreme temperatures, drought, salinity, and pathogen attacks, making melatonin a promising candidate for enhancing plant resilience. Furthermore, the interplay between melatonin and other phytohormones, such as auxins, cytokinins, and abscisic acid, adds complexity to its regulatory functions in response to stress. Melatonin's ability to modulate hormone signaling pathways presents exciting possibilities for fine-tuning plant stress responses and optimizing growth in adverse conditions. This chapter comprehensively elucidated the synergistic effects of melatonin-mediated plant growth and development to fully understand its role in plant physiology and stress mitigation.

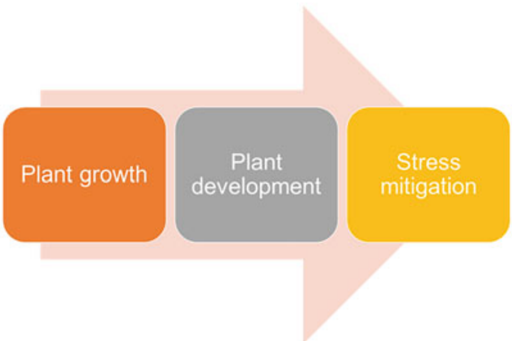
Keywords

Anti-stress manager · Antioxidant · Biostimulant · Circadian rhythm · Hormonal cross-talk · Heavy metal toxicity

11.1 Introduction

Melatonin (N-acetyl-5-methoxy-tryptamine) is a ubiquitous and pleiotropic indoleamine neurohormone primarily known for regulating the circadian rhythm, sleep-wake cycle, and immune function in mammals, including humans (Arnao and Hernández-Ruiz 2019b, 2021). However, it was also identified and quantified in plants in 1995 (Dubbels et al. 1995; Hattori et al. 1995). Melatonin has been detected in various plant species, including both angiosperms and gymnosperms. Melatonin regulates multifunctional processes in plants (Fig. 11.1), including growth,

Fig. 11.1 Major role of melatonin in plants



development, and stress responses (Menhas et al. 2021a; Zeng et al. 2022b). Melatonin has been found to regulate seed germination, root elongation, flowering, and fruit senescence, which are crucial for crop production (Arnao et al. 2022; Altaf et al. 2022c, b). Likewise, melatonin promotes cell division and elongation, which can increase biomass and plant yield. Melatonin may help plants adapt to changing environmental conditions by regulating physiological processes (Zeng et al. 2022b; Altaf et al. 2022a).

Furthermore, melatonin act as a signaling molecule that can protect plants against various abiotic stresses such as drought, high salinity, cold, high temperature and heavy metal toxicity, among others (Zeng et al. 2022b). Plant protection is achieved through its potent antioxidant properties, which can scavenge reactive oxygen species (ROS) as well as reactive nitrogen species (RNS) and reduce oxidative damage to plant cells (Arnao and Hernández-Ruiz 2019a). Reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2), superoxide ($O_2^{\cdot-}$), and hydroxyl radical ($OH^{\cdot}$), are produced in plants as by-products of cellular metabolism and can accumulate to toxic levels and cause oxidative damage to plant cells, leading to cellular dysfunction and death due to various stresses such as drought, high salinity, and heavy metal-induced toxicity (Hasanuzzaman et al. 2012; Sachdev et al. 2021). Melatonin can scavenge these ROS and reduce oxidative damage to plant cells, thus protecting plants against these stresses. Recent studies have shown that melatonin can mitigate the adverse effects of environmental stressors on plant growth and development (Asif et al. 2020; Menhas et al. 2022; Nawaz et al. 2020). Moreover, melatonin modulates the expression of stress-related genes and proteins, such as heat shock proteins and enzymes involved in stress-signaling pathways. By regulating gene expression and protein synthesis, melatonin enhances plant tolerance to stress conditions. Melatonin may play a role in plant development and stress responses by regulating gene expression, antioxidant activity, hormonal cross-talk, and other cellular processes (Ayyaz et al. 2022; Erland et al. 2016). For instance, melatonin treatment improved the drought tolerance of rice plants by regulating the expression of stress-related genes (Luo et al. 2022; Zhang et al. 2022a).

Melatonin has also been shown to enhance the tolerance of plants to drought stress by regulating water uptake, reducing water loss through transpiration, and increasing antioxidant activity (Luo et al. 2022). Similarly, melatonin can protect plants from salinity stress by regulating ion transport and reducing oxidative damage caused by salt accumulation (Altaf et al. 2021a). Melatonin also protects plants exposed to heavy metals, such as cadmium (Cd) and lead (Pb), by reducing their absorption and enhancing detoxification mechanisms (Menhas et al. 2022; Xie et al. 2021a). Furthermore, melatonin is important in plant defense against biotic stresses, such as pathogen infections (Moustafa-Farag et al. 2019; Tiwari et al. 2020). It does so by activating plant defense mechanisms and by regulating the production of phytohormones, which are chemical messengers that control plant growth and development (Tiwari et al. 2021b).

One of the ways melatonin can help plants cope with environmental stress is through its synergistic effect with other plant hormones, such as abscisic acid (ABA), indole-3-acetic acid (IAA), cytokinins, and gibberellins (Altaf et al. 2023;

Khan et al. 2022; Kumar et al. 2022). ABA is known to be involved in stress responses, such as drought and salinity, while IAA is involved in plant growth and development. However, cytokinins regulate cell division and differentiation. Treating tomato plants with melatonin and IAA increased growth and higher anti-oxidant activity under salt stress (Zhan et al. 2019). Melatonin enhances the effect of auxins on root elongation while inhibiting the effect of cytokinins on shoot growth (Wang et al. 2022a; Lal et al. 2022b, e). On the contrary, studies have shown that melatonin can promote plant growth and development by increasing cytokinin levels while controlling growth-inhibiting hormones such as ethylene or abscisic acid (Hernández-Ruiz et al. 2005). Therefore, melatonin can be useful in mitigating the adverse effects of both internal and external cues on plant growth and development through its synergistic effects with other plant hormones. Nonetheless, additional research is needed to understand the mechanisms underlying these interactions and their implications for plant physiology and agriculture (Lal et al. 2022a, b, c, d).

Another critical role of melatonin in plants is to regulate the circadian rhythm, which is important for adapting to changing environmental conditions (Ahn et al. 2021). The circadian rhythm is a 24-h biological cycle that controls various physiological processes, including growth and development. Melatonin helps to synchronize the circadian rhythm of plants with environmental cues such as light and temperature, which in turn influences growth and development (Agathokleous et al. 2019; Ahn et al. 2021). Nonetheless, the regulation of melatonin-mediated plant growth and development is a complex process involving several factors, including environmental factors and cross-talk with other plant hormones. Various environmental factors, including light, temperature, and nutrient availability, can influence plant melatonin levels (Liu et al. 2022). Similarly, melatonin biosynthesis is controlled by a complex interplay of various hormones and factors, which affect its production. In summary, melatonin plays a multifunctional role in plants, regulating growth and development, as well as stress responses. Understanding these functions may lead to developing new strategies for enhancing crop productivity and improving plant stress tolerance.

11.2 Melatonin: Provoking Defense Mechanisms against Various Stresses in Plants

Melatonin, a ubiquitous molecule in plants, has been shown to possess various physiological roles, including antioxidant and anti-stress manager (Khan et al. 2020). The ability of melatonin to provoke defense mechanisms against multiple stresses in plants (Fig. 11.2) highlights its potential as a natural and sustainable tool for enhancing plant tolerance and productivity under adverse environmental conditions (Sati et al. 2023; Sun et al. 2021; Tiwari et al. 2020).

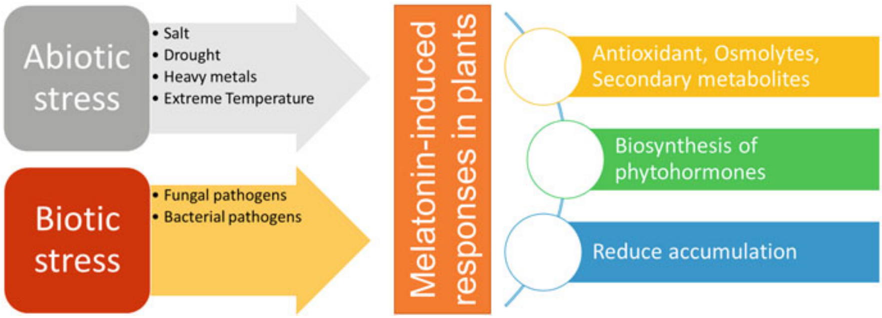


Fig. 11.2 Melatonin provokes defense against multiple stresses in plants

11.2.1 Melatonin Against Abiotic Stressors

In plants, melatonin has been shown to have numerous functions, including acting as a signaling molecule in response to various stresses, including drought, salinity, cold, temperature extremes, and heavy metals. Several researchers (Tan et al. 2012; Li et al. 2019) found that melatonin enhanced the tolerance of tomato plants to hydrogen peroxide (H_2O_2)-induced oxidative stress by regulating the expression of antioxidant-related genes Altaf et al. 2020, 2022d, thereby protecting plants from oxidative stress. Similar studies regarding melatonin-induced tolerance mechanism are given below:

11.2.2 Melatonin Application Alleviates Drought Stress

Melatonin acts as a central regulator of the plant response to drought stress (Altaf et al. 2022d). Exogenous melatonin significantly increased drought tolerance in several plants, including tomato, watermelon, maize, rice, and grapevine (Altaf et al. 2022d; Li et al. 2019; Wang et al. 2022b; Zhao et al. 2022), by improving biomass, photosynthetic rates, stomatal regulation, and water use efficiency and the activities of antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) as well as relieving ROS-induced oxidative stress than untreated plants. Melatonin has been shown to regulate the activity of aquaporins, which are membrane proteins that facilitate water transport across cell membranes in plants (Mandal et al. 2022). Exogenous application of melatonin increases the expression of a specific aquaporin gene (PIP2;1) in plants (Jogawat et al. 2021; Zhang et al. 2020), leading to increased water uptake and improved drought tolerance. Melatonin has also been shown to reduce water loss through transpiration (Muhammad et al. 2022; Mishra et al. 2022), which is the process by which plants lose water through their leaves. Exogenous application of melatonin increased the activity of several antioxidant enzymes (e.g., superoxide dismutase, catalase, and peroxidase) in cucumber plants under drought conditions, leading to improved drought tolerance (Zhang et al. 2020).

Furthermore, melatonin treatment increased the expression of genes involved in water uptake and transport, osmotic adjustment, and antioxidant defense in the plants (Tiwari et al. 2021a; Yang et al. 2022), which helped to maintain the plant's physiological functions and reduce water loss under drought conditions (Nandy et al. 2022). Additionally, melatonin triggers a cascade of events leading to enhanced drought tolerance in the plants (Sharma and Zheng 2019), including the activation of key responsive genes/enzymes involved in the stress-signaling pathway and production of abscisic acid (ABA), a well-known hormone in plant drought response. Melatonin induces the synthesis and signaling of ABA, which in turn (Naz et al. 2022b, b). Furthermore, a study by Arnao and Hernández-Ruiz (2014) found that melatonin treatment reduced lipid peroxidation (a process that produces harmful free radicals and damages cell membranes) in pepper plants under water stress conditions. Overall, these studies suggest that melatonin plays a vital role in helping plants to cope with drought stress by regulating various physiological and molecular processes, including antioxidant defense, water use efficiency, gene expression and reducing water loss through transpiration, highlighting the potential of melatonin as a tool for improving plant stress tolerance, productivity and sustainability in the face of climate change.

11.2.3 Melatonin and Salt Stress

Salinity or salt stress is a major constraint of crop production that often causes ROS production in plants, leading to lipid peroxidation, reduced photosynthetic processes, and plant development (Hayat et al. 2020a, c; Tiwari et al. 2022a, b). Compared to untreated plants, melatonin-treated wheat and tomato plants had higher germination rates, longer roots, higher biomass accumulation, hyperactivities of antioxidant enzymes, and lower ROS-induced repercussions under saline conditions (Altaf et al. 2021a; Zafar et al. 2019). Melatonin reduces ROS levels and improves plant growth and yield under salt stress (Hussain et al. 2022). Several studies (Altaf et al. 2021a; Hussain et al. 2022) investigated that melatonin treatment significantly reduced the accumulation of ROS and lipid peroxidation products as well as enhanced the activity of antioxidant enzymes in salt-stressed tomato and maize plants, thus protecting the plants from oxidative damage and improving salt tolerance. Exogenous application of melatonin could enhance the salt tolerance of various plants (Ali et al. 2021; Wei et al. 2015; Yang et al. 2020), while melatonin-deficient mutants showed reduced salt tolerance. Melatonin interacts with a protein called calmodulin, which regulates calcium signaling in plants (Hardeland 2009). Specifically, melatonin-mediated activation of calmodulin leads to an increase in the expression of genes encoding for proteins involved in ion transport and homeostasis, such as SOS1 and NHX1 (Arnao and Hernández-Ruiz 2019a; Arnao and Hernández-Ruiz 2015). These proteins are known to maintain ion balance in cells under salt-stress conditions. Similarly, Chen et al. (2018) examined the role of melatonin in regulating ion transport in salt-stressed maize seedlings. Melatonin treatment reduces the accumulation of sodium ions (Na^+) in the roots and shoots of salt-stressed plants as well as increases the activity of plasma membrane H^+-ATPase (involved in pumping out excess Na^+ ions from plant cells), suggesting that melatonin can regulate ion transport in plants (Li et al. 2017), thereby reducing the toxic effects of salt stress.

Melatonin increases the expression of genes involved in ROS scavenging and decreases the expression of genes involved in ROS production in salt-stressed sunflower plants (Arora and Bhatla 2017). Overall, these studies suggest that melatonin plays an important role in helping plants cope with salt stress by regulating ion transport, increasing antioxidant activity and reducing oxidative damage caused by salt accumulation. Further research is needed to fully understand the mechanisms underlying the protective effects of melatonin in plants under salinity stress.

11.2.4 Melatonin Treatment under Temperature Fluctuations

Heat stress can cause protein denaturation and aggregation, leading to cellular damage and ultimately cell death (Wahid et al. 2007). Melatonin plays a protective role in plants exposed to extreme temperatures (Bajwa et al. 2014). Melatonin treatment improved the survival rate of *Cucumus sativus*, *Camellia sinensis* and tomato plants under cold stress by maintaining higher levels of antioxidant enzymes and protective compounds (such as proline and soluble sugars) coupled with lower ROS levels and lipid peroxidation products, indicating reduced oxidative stress and improved cold tolerance in plants (Korkmaz et al. 2021; Li et al. 2018; Marta et al. 2016). Both heat and cold stress increase ROS production, leading to oxidative damage and cell death. Interestingly, exogenous melatonin reduced ROS levels and improved plant survival under extreme temperatures (Murch and Erland 2021; Sharma et al. 2020b). Zhang et al. (2020) observed that melatonin protected cherry reddish plants from high-temperature stress by regulating the expression of genes related to antioxidant defense and heat shock proteins (Jia et al. 2020). However, treating plants with melatonin increases their thermos-tolerance capability by inducing the expression of heat shock proteins (HSPs) (Xia et al. 2021). Melatonin treatment increased the binding of OsWRKY (a transcription factor that regulates the expression of HSPs) to the promoter regions of HSP genes, leading to increased transcription and expression of HSPs in rice plants (Bakshi and Dewan 2013). HSPs are a group of proteins that protect cells from heat damage by facilitating proper protein folding and preventing protein aggregation (Wang et al. 2004). In summary, melatonin plays an important role in helping plants cope with temperature extremes by acting as a protective agent and signaling molecule by inducing the expression of HSPs in plants.

11.2.5 Melatonin and Heavy Metal Toxicity

Heavy metal stress is a severe environmental stress that affects plant growth and productivity (Hayat et al. 2020b; Menhas et al. 2020; Menhas et al. 2021b). Arsenic (As) and cadmium (Cd) are the most toxic heavy metals that can accumulate easily in plants, causing damage to various cellular components and reducing plant growth and yield (Li et al. 2020; Menhas et al. 2021b). Exogenous application of melatonin improves the growth and heavy metal tolerance of plants by enhancing antioxidant defense systems and reducing oxidative damage (Hoque et al. 2021; Moustafa-Farag et al. 2020). Xie et al. (2021b) investigated the molecular mechanisms underlying the protective effects of melatonin against arsenic toxicity in rice plants. The researchers found that melatonin treatment modulated the expression of genes involved in stress response pathways, including those related to antioxidant defense and detoxification. Melatonin alleviated Pb toxicity by reducing Pb accumulation and enhancing the antioxidative defense system in safflower plants (Namdjoyan et al. 2020). Also, melatonin treatment reduced Cd accumulation in plant tissues and improved plant growth under Cd stress conditions (Menhas et al. 2021a, 2022). Melatonin application improved plant growth and reduced the adverse effects of cadmium toxicity via antioxidant and detoxifying properties, protecting plants from heavy metal-induced oxidative stress. A study by Wang et al. (2019) investigated the role of melatonin in protecting tobacco plants from oxidative damage induced by cadmium stress. The results showed that melatonin treatment significantly reduced the accumulation of ROS and improved the activity of antioxidant enzymes, thus protecting the plants from cadmium-induced oxidative damage.

Exposure of tomato plants to multi-metal stress led to a significant decrease in growth and photosynthesis, as well as an increase in oxidative stress, as evidenced by an increase in reactive oxygen species (ROS) production and lipid peroxidation (Hasan et al. 2015; Li et al. 2016; Zhang et al. 2022b). However, pre-treatment with exogenous melatonin alleviated Cd-induced toxicity (Hasan et al. 2015; Li et al. 2016; Zhang et al. 2022b), as indicated by an increase in growth, photosynthesis, and inhibited Cd-induced ROS production by upregulating the expression of genes encoding enzymes involved in ROS scavenging and/or antioxidant defense system, such as SOD, CAT, ascorbate peroxidase (APX), peroxidase (POD), glutathione S-transferase (GST), and glutathione peroxidase (GPX). Moreover, melatonin treatment also upregulates the expression of genes involved in Cd uptake, transport and detoxification, such as the metal transporter IRT, Nramp5 and the heavy metal ATPase HMA3, which decreased Cd accumulation in the plants (Gu et al. 2021). Another study (Xu et al. 2020) on radish plants showed that melatonin played a role in regulating cadmium transport from roots to shoots by increasing the expression of genes involved in cadmium sequestration in roots, suggesting melatonin can help plants avoid the toxic effects of HMs by limiting its accumulation in the aerial parts. Moreover, melatonin enhances the plant's ability to tolerate HMs stress by increasing the production of phytochelatins (PCs) and metallothioneins (MET), which are important metal chelators. PC and MET can bind to and detoxify HMs, preventing them from damaging cellular components (Menhas et al. unpublished). Melatonin has also been found to improve the uptake and translocation of essential nutrients, such as nitrogen, phosphorus, and potassium, in plants under cadmium stress (Altaf et al. 2022b; Altaf et al. 2022e). This is important because cadmium can interfere with nutrient uptake and cause nutrient deficiencies in plants, leading to reduced growth and yield. In summary, melatonin is crucial in protecting plants from HM-induced damage by enhancing antioxidant defense systems, activating the expression of detoxification genes, regulating the transport of cadmium, and increasing the production of metal chelators. However, further research is needed to determine the optimal concentration and application method of melatonin for different plant species and HMs concentrations. The exact mechanism by which melatonin confers HM-tolerance in plants is not fully understood, however, it may involve various biochemical and physiological pathways, including regulation of gene expression, modulation of hormone levels, and enhancement of antioxidant systems.

11.3 Melatonin against Biotic Stressors

Biotic stress devastates worldwide agricultural production and increases the risk of hunger in several regions (Peterson and Higley 2000). Plants tolerate biotic stresses through a variety of mechanisms, including pathogen-associated molecular patterns (PAMPs) that activate immunity and plant resistance (R) proteins (Moustafa-Farag et al. 2019). Nonetheless, melatonin gained significant interest in plant growth regulation and increasing plant resistance to biotic stressors (Moustafa-Farag et al. 2019; Singh and Singh 2018). Although much research has been conducted on the role of melatonin in plant tolerance to abiotic stresses, its role in biotic stress remains unknown and requires clarification. Melatonin is critical in enhancing plant resistance against biotic stresses, such as pathogen infections. Exogenous melatonin significantly reduces disease symptoms and bacterial growth compared to untreated plants (Tiwari et al. 2021b; Zhao et al. 2021a). Notably, melatonin elicits the production of reactive oxygen species (ROS) in plants as a secondary signal, which can help to kill invading pathogens. Treating plants with melatonin led to increased ROS production and enhanced resistance to infection with the fungal pathogen *Magnaporthe oryzae* (Li et al. 2023). Melatonin has also been shown to regulate the expression of genes involved in plant defense, such as those encoding pathogenesis-related (PR) proteins (Guo et al. 2022).

Additionally, melatonin has been shown to stimulate the production of phytohormones, such as salicylic acid and jasmonic acid, which are chemical messengers involved in regulating plant defense responses (Arnao and Hernández-Ruiz 2018a; Tiwari et al. 2021b). Melatonin has been shown to inhibit auxin production, a hormone promoting plant growth. By doing so, melatonin can redirect the plant's resources toward defense mechanisms instead of growth. Melatonin-treated plants showed increased production of both salicylic acid and jasmonic acid and enhanced resistance to infection with the bacterial pathogen *Pseudomonas syringae* (Zeng et al. 2022a). Exogenous application of melatonin to tomato plants infected with the fungal pathogen *Botrytis cinerea* led to reduced disease symptoms and increased expression of defense-related genes (Liu et al. 2019). Recent studies (Jayarajan and Sharma 2021; Zeng et al. 2022a; Zhao et al. 2021a) showed that exogenous application of melatonin increased the resistance of tomato and rice plants to the pathogenic fungus *Fusarium oxysporum* and bacterial pathogen *Xanthomonas oryzae* by increasing the production of ROS and pathogenesis-related (PR) proteins combined with regulating the expression of genes involved in the biosynthesis of phytohormones. Sum of all, melatonin enhances plant resistance to pathogens by inducing the production of ROS and phytohormones and directly suppressing pathogen growth and disease symptoms.

11.4 Melatonin: A Multifunctional Factor in Plants

Melatonin is a multifunctional factor in plants that orchestrate various physiological processes and/or functions in plants (Fan et al. 2018). Melatonin modulates plant responses to multiple stressors, such as high salt levels, drought, and temperature extremes (Arnao et al. 2022). Melatonin has been shown to enhance photosynthesis, increase chlorophyll content, and improve carbon assimilation in plants, all of which can improve plant growth and development (Arnao and Hernández-Ruiz 2006). The exogenous application of melatonin increased the length, weight and photosynthetic capacity of maize seedlings under normal and salinity stress conditions (Ahmad et al. 2021), suggesting that melatonin can act as a growth regulator and anti-stress manager in plants. Melatonin upregulates the expression of genes involved in seed germination and root elongation while downregulating the expression of genes involved in leaf senescence (Arnao and Hernández-Ruiz 2015). Melatonin helps to scavenge reactive oxygen species (ROS) and reduce oxidative damage (Arnao and Hernández-Ruiz 2019a), which can help to maintain plant health and productivity. Melatonin also increases the size and number of flowers and fruits (Arnao and Hernández-Ruiz 2020; Verde et al. 2022). Melatonin can also be used as a natural preservative in fruits and vegetables (Feng et al. 2022). Melatonin delays the ripening of fruits such as tomatoes, bananas, and strawberries by inhibiting the expression of genes that promote ripening (Nawaz et al. 2020; Wu et al. 2021), resulting in longer shelf life and improved quality of the fruit. Melatonin can act as an antioxidant that can delay the ripening process by inhibiting the production of ethylene (Gao et al. 2022). In contrast, several studies have shown that melatonin treatment can stimulate the biosynthesis of ethylene (Sun et al. 2020; Verde et al. 2022, 2023), which is a key hormone involved in the ripening process of many fruits and vegetables. Sun et al. (2020) observed that exogenous melatonin treatment increased ethylene production by upregulating the expression of genes (including ACS2 and ACO1) involved in ethylene biosynthesis, which accelerated the ripening of tomato fruits. Similarly, melatonin treatment not only increased the expression of genes involved in ethylene biosynthesis and ripening in fruits but also enhanced the activity of enzymes involved in ethylene biosynthesis, including ACC oxidase and ACC synthase (Arnao and Hernández-Ruiz 2021; Arnao and Hernández-Ruiz 2018b). Melatonin treatment has also been shown to improve the quality of fruits and vegetables by reducing weight loss, maintaining firmness, and preserving color (Liu et al. 2018; Onik et al. 2021), thus increasing the market value of the produce as well as reduce waste. Similarly, treating strawberries with melatonin resulted in a delay in the decay and softening of the fruit, as well as an increase in antioxidant activity and overall quality (Liu et al. 2018), which suggest that melatonin has great potential as a natural and environmentally friendly way to regulate the postharvest management of fruits and vegetables.

The role of melatonin in regulating flower development such as delayed flower senescence and prolonged flower lifespan were also investigated (Arnao and Hernández-Ruiz 2020), suggesting its potential applications in horticulture. Studies have shown that melatonin can regulate the expression of genes such as constants, (CO) and flowering locus T (FT) involved in the flowering process (Arnao and Hernández-Ruiz 2020; Shi et al. 2016), essential for the transition from vegetative growth to reproductive growth. Melatonin has also been shown to interact with other signaling molecules, such as gibberellins and abscisic acid, to regulate flowering time (Arnao and Hernández-Ruiz 2018a). The regulation of flowering time is critical for crop production, as it affects the yield and quality of crops. The timing of flowering determines when the plant will produce seeds or fruits, and if the flowering time is not properly regulated, the plant may not produce enough seeds or fruits, or the quality of the seeds or fruits may be compromised. Therefore, understanding the role of melatonin in regulating flowering time could have important implications for improving crop production and food security. Melatonin can also modulate stress-related hormonal signaling pathways, such as those involving abscisic acid (ABA), jasmonic acid (JA), and salicylic acid (SA), to enhance plant stress tolerance (Arnao and Hernández-Ruiz 2018a).

Additionally, melatonin regulates plant circadian rhythms (Ahn et al. 2021; Kolář and Macháčková 2005), which can help plants synchronize their growth and development with the day-night cycle and other environmental cues. The mechanism by which melatonin regulates the circadian rhythm in plants is not yet fully understood and is yet in the initial stage. Melatonin is a potent antioxidant, protecting plant cells from oxidative damage caused by environmental stressors such as UV radiation and high temperatures (Back 2021; Tan et al. 2015). This, in turn, contributes to the integrity of the plant's circadian rhythm. Similar studies have shown that melatonin levels in plants exhibit diurnal fluctuations and may play a role in regulating the expression of genes involved in circadian rhythms (Pandi-Perumal et al. 2006). The role of melatonin in regulating the circadian clock was thoroughly investigated in plants (Chang et al. 2021; Sun et al. 2021). The results of the study revealed that melatonin treatment altered the expression of clock genes and impacted the rhythms of leaf movement and chlorophyll fluorescence in the plants. One key component of the plant circadian clock is a set of transcription factors called Circadian Clock-Associated 1 (CCA1) and Late Elongated Hypocotyl (LHY) (Wang and Tobin 1998). These proteins interact with other clock genes to form a complex regulatory network that controls the timing of gene expression and physiological processes in plants. In addition, the circadian clock also plays a role in regulating plant responses to light (Liu et al. 2020). The accumulation of ROS over time leads to oxidative

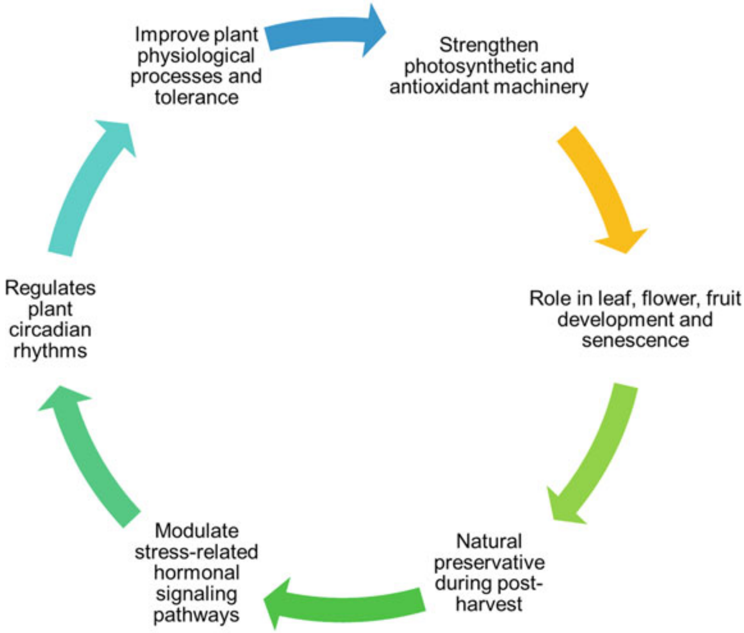


Fig. 11.3 Multifunctional role of melatonin in plant growth, development, and stress tolerance

damage to cells and tissues, contributing to the aging process (Finkel and Holbrook 2000). Meanwhile, melatonin could slow aging (Shi et al. 2019; Zhao et al. 2021b). Therefore, melatonin is multifunctional in plant stress tolerance by regulating various physiological, biochemical and molecular processes (Fig. 11.3). Its ability to promote growth, development, and stress tolerance is critical to plant physiology.

11.5 Synergistic Response of Melatonin Biosynthesis with Other Hormones

Melatonin is a multifunctional molecule that regulates plant growth and development in addition to its well-known antioxidant properties, which are directly linked with the interaction and/or cross-talk with other plant hormones such as auxin, cytokinins, abscisic acid, gibberellins (GA), jasmonic acid (JA), salicylic acid (SA), ethylene, and brassinosteroids (BRs), among others (Arnao and Hernández-Ruiz 2021; Arnao and Hernández-Ruiz 2018a). Plant hormones play a crucial role in coordinating various physiological and developmental processes in plants, including growth, differentiation, and response to environmental stimuli. Growing evidence shows that melatonin interacts with various plant hormones to regulate plant growth and development (Raza et al. 2022; Sun et al. 2021). Exogenous melatonin upregulated the expression of PIN-FORMED 1 (PIN1) gene involved in auxin biosynthesis and transport in *Arabidopsis thaliana* (Arnao and Hernández-Ruiz

2017; Zia et al. 2019), leading to an increase in auxin levels and subsequent cell elongation and root growth. Auxins are primarily responsible for regulating cell elongation and division, and they also play a role in apical dominance, root development, and fruit ripening (Gomes and Scortecci 2021). Studies have found that exogenous melatonin application can increase the endogenous levels of auxins, leading to enhanced root growth and development in various plant species (Altaf et al. 2021b; Arnao and Hernández-Ruiz 2018a).

Cytokinins, on the other hand, are known to promote cell division and differentiation and play an important role in regulating plant growth and development (Werner and Schmülling 2009). Several studies (Erland et al. 2018; Zhang et al. 2017) have investigated melatonin's effects on the biosynthesis of cytokinins and abscisic acid. Melatonin treatment increased the levels of cytokinins in lettuce seedlings, which was attributed to higher gene expression in cytokinin biosynthesis (Yu et al. 2022; Zhan et al. 2019).

Abscisic acid (ABA) is a plant hormone that is involved in many physiological processes, including seed dormancy and stress responses (Parwez et al. 2022). Melatonin has been shown to increase the biosynthesis of ABA and promote ABA-mediated stomatal closure (Wang et al. 2021), thereby reducing water loss and improving drought or extreme temperature tolerance in plants. Melatonin-treated tomato plants showed enhanced drought tolerance, as evidenced by better leaf water status, higher photosynthetic efficiency, and lower oxidative stress than control plants (Mushtaq et al. 2022). Likewise, melatonin promotes the accumulation of ABA and enhances Arabidopsis seedlings' sensitivity to ABA during seed germination and early seedling growth (Lv et al. 2021). This effect was attributed to the increased expression of the ABA biosynthetic gene NCED3 and the ABA signaling gene ABI5 (Lv et al. 2021; Yin et al. 2022).

Furthermore, it has been discovered that melatonin enhances gibberellin biosynthesis and signaling in Arabidopsis, which was mediated by the upregulation of the gibberellin biosynthetic gene GA3ox1 and the GA receptor gene GID1b (Yang et al. 2021). Melatonin has been demonstrated to increase the accumulation of jasmonic acid (JA) and its derivatives in plants subjected to salinity stress, as well as the expression of genes involved in JA biosynthesis (Ding et al. 2022; Khan et al. 2022). The biosynthesis of flavonoids in tea plants is controlled by melatonin's interaction with jasmonates in a similar way (Di et al. 2019). It has been discovered that melatonin boosts the capacity of SA to endorse the pathogen defense response in plants (Arnao and Hernández-Ruiz 2019b). This effect was mediated by the upregulation of the SA biosynthetic gene ICS1 and the SA signaling gene NPR1 (Zhao et al. 2021a). Melatonin delay fruit ripening by inhibiting ethylene biosynthesis and signaling in fruits via downregulation of the ethylene biosynthetic genes (Arnao and Hernández-Ruiz 2020). Melatonin was also involved to enhance the sensitivity of *Arabidopsis* seedlings to BRs during hypocotyl elongation (Xiong et al. 2019). Together, melatonin interacts with various plant hormones to regulate different facets of plant growth and development. Further study is necessary to fully elucidate the mechanisms underlying these interactions and their potential agricultural applications because the interactions between melatonin and other plant hormones are complicated and poorly understood.

11.6 Regulation of Melatonin-Mediated Plant Growth and Development

Melatonin is a hormone that is widely distributed in all living things, including plants, animals, and microorganisms. It is well known to play a significant part in controlling a number of physiological processes, such as the immune system, metabolism, and the sleep-wake cycle. In recent years, research has shed light on the role of melatonin in plant growth and development. Studies have shown that melatonin regulates plant growth and development by modulating various physiological processes, including photosynthesis, antioxidative defense, and gene expression (Altaf et al. 2022d; Sharma et al. 2020a). For instance, melatonin improves photosynthesis in plants by regulating the expression of genes involved in photosynthesis and chlorophyll synthesis (Jahan et al. 2021).

Additionally, melatonin enhances the antioxidant defense system in plants by increasing the activity of antioxidant enzymes and reducing oxidative damage (Khan et al. 2020), suggesting a crucial role of melatonin in regulating plant responses to environmental stress. Melatonin mitigates the negative effects of abiotic stressors such as drought, salt, and heavy metal toxicity (Kul et al. 2019). On the other hand, melatonin also augments plant resistance to biotic stressors such as pathogens and herbivores (Moustafa-Farag et al. 2019). However, the regulation of melatonin-mediated plant growth and development is a complex process that involves several factors, including light, temperature, plant hormones, and circadian rhythms. Light is one of the major factors in regulating plant melatonin biosynthesis and metabolism (Hwang et al. 2020). In plants, exposure to different wavelengths of light, such as blue light and red light, has been shown to increase melatonin levels (Tan and Reiter 2020).

Additionally, light quality and intensity have been shown to affect the expression of genes involved in melatonin biosynthesis and metabolism (Li et al. 2021). Temperature is another important factor that affects melatonin levels in plants. Byeon and Back (2014) concluded that high temperatures could increase melatonin levels in rice seedlings. Additionally, cold stress has been shown to induce the expression of genes involved in melatonin biosynthesis (Fu et al. 2017). Plant hormones also play a key role in the regulation of melatonin-mediated plant growth and development (Arnao and Hernández-Ruiz 2018a). Last but not least, one of the critical roles of melatonin-mediated plant growth and development is to regulate the circadian rhythm (Ahn et al. 2021). Understanding how melatonin affects plants may help researchers establish creative solutions to boosting plant growth and productivity in horticulture and agricultural sectors.

11.7 Conclusion and Future Perspectives

In conclusion, using melatonin in agriculture has great potential for improving crop production and sustainability, particularly in the face of increasing environmental stressors. Based on current research, it is clear that melatonin plays a vital role in the growth and development of plants, particularly in mitigating the harmful effects of stress. Melatonin has been found to act as a potent antioxidant, reducing the accumulation of reactive oxygen species (ROS) and reactive nitrogen species (RNS) and protecting plants from oxidative damage. It also regulates plant growth, modulates gene expression, and enhances plant tolerance to both biotic and abiotic stressors. The effects of melatonin on crop yield and quality should be studied in more detail. Future research could identify the specific mechanisms by which melatonin promotes plant growth and development, particularly in stress conditions. The mechanisms by which melatonin regulates plant growth and development are complex and multifaceted, involving interactions with various signaling pathways and gene regulatory networks. The synergistic effect of melatonin with other plant hormones and its ability to scavenge ROS and regulate gene expression makes it a promising candidate for plant growth and stress mitigation in plants.

Additionally, studies are required to determine the optimal concentration, application method, and timing of melatonin treatment for different plant species and stress types. By exploring the potential of melatonin with other plant growth regulators, we can develop more resilient crops that are better equipped to withstand environmental stresses and provide food security for future generations. Moreover, applying melatonin in combination with genetic engineering techniques could potentially enhance plants' stress tolerance and growth. Continued research in this area could lead to the development of more effective and sustainable agricultural practices.

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