Melatonin-Mediated Regulation of Germination, Plant Establishment, and Vegetative Development

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Abstract

Plants growth and development is hampered by fluctuation in both edaphic and atmospheric conditions. Such changes stimulate plants signaling mechanisms and as a result plants produce chemicals to sustain under stressful conditions. One of the crucial natural products produced by the plants is melatonin, an incredibly effective antioxidant. However, primarily melatonin was recognized as sleep promoting agent present in animal brain linked to the regulation of sleep-wake cycle. In plants this product is synthesized in chloroplast and mitochondria and is also known as amine hormone. Melatonin plays a crucial role in plants by serving as first line of defense against internal and external oxidative stresses. It is believed that plants, which lack the ability to move like animals do, have significantly greater amounts of melatonin as a way of compensating for the harsh surroundings they must endure. In plants life cycle one of the important developmental stages is seed germination which is regulated by complex signaling mechanisms. Melatonin plays an important role as signaling molecule which improves seed germination under stressful conditions. Melatonin is known to facilitate physiological control systems, improve seed germination, and stimulate crop growth under stress. Melatonin can effectively alleviate the suppression of seed germination by boosting osmotic regulators and correcting ion homeostasis during salt stress. Melatonin also plays a significant role in regulating the

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R. Kumar et al. (eds.), *Melatonin in Plants: A Regulator for Plant Growth and Development*, https://doi.org/10.1007/978-981-99-6745-2_3

metabolism of nitrogen and the composition of mineral elements, which lessens the growth-inhibiting effects of nitrate stress. The major focus of this chapter will be on how melatonin affects plant growth, seed germination, and vegetative development.

Keywords

Melatonin · Germination · Seedling establishment · Development

3.1 Introduction

Melatonin, a naturally occurring compound in plants, has a similar function as it does in animals—regulating circadian rhythms. Tryptophan, an amino acid, is the main source of melatonin synthesis in plants, and it can be found in various plant parts such as roots, leaves, fruits, and seeds. Melatonin can play a vital role in different plant processes like growth, development, stress responses, and immune system function according to scientific studies. Changing climate conditions are causing a decline in growth and yield of plants in various regions. Numerous environmental factors, including salinity, alkalinity, drought, temperature (both high and low), and metals, can have negative impacts on plant productivity, yield, and quality (Altaf et al. 2022b). Abiotic stress can affect horticultural crops differently, with solanaceous plants being particularly vulnerable, particularly during their reproductive stages, including seed formation, flowering, and fruiting (Francini and Sebastiani 2019). Heavy metals, such as vanadium and nickel, have been shown to significantly affect the root system and photosynthesis of pepper (Altaf et al. 2022a, d). Similarly, cadmium toxicity has been reported to cause deformation of tomato roots and hinder mineral and nutrient absorption (Borges et al. 2019). Salt stress can result in reduced chlorophyll levels, an increase in reactive oxygen species (ROS), malondialdehyde (MDA), and electrolyte leakage (EL), leading to oxidative damage to tomatoes (Khan et al. 2012).

Plants in various regions are facing decreased growth and yield due to changing climate conditions. Environmental factors such as salinity, alkalinity, drought, temperature (both high and low), and metals can impact the productivity, yield, and quality of the plants (Altaf et al. 2022d). Abiotic stress can affect horticulture crops differently, with solanaceous plants being particularly susceptible, especially during their reproductive stages of seed formation, flowering, and fruiting (Francini and Sebastiani 2019). Heavy metals like vanadium and nickel can seriously affect the root system and photosynthesis of pepper (Altaf et al. 2022a, d). Similarly, cadmium toxicity can deform tomato roots and prevent mineral and nutrient absorption (Borges et al. 2019). Salt stress can lead to a decrease in chlorophyll, increase in reactive oxygen species (ROS), malondialdehyde (MDA), and electrolyte leakage (EL), causing oxidative damage to tomatoes (Khan et al. 2012).

When plants are under drought stress, their proline content, MDA content, hydrogen peroxide (H_2O_2) content, and antioxidant enzyme activity increase, while eggplant growth characteristics, protein content, and pigment content decrease. Additionally, salt stress can have a negative impact on the growth and development of plants such as petunias (Krupa-Małkiewicz and Fornal 2018). Studies have shown that a combination of drought and heat stress can lead to decreased tobacco leaf photosynthesis and increased leaf temperature (Rizhsky et al. 2002). Due to these environmental challenges, the horticulture industry is constantly exploring new technologies and methods to minimize their impact and ensure high-quality, sustainable products. Developing new cultivars with improved abiotic stress tolerance could significantly impact the global food supply. Scientists are researching various plant hormones that help plants respond better to these stresses.

Melatonin is a recently discovered, plant hormone believed to play a crucial role in regulating plant growth (Arnao and Hernández-Ruiz 2019; Altaf et al. 2021). Recent studies show that melatonin has positive effects on seed germination, root growth, flowering, nutrient uptake, regulating antioxidant levels, and balancing mineral homeostasis in Solanaceae crops (Sarafi et al. 2017; Tiwari et al. 2020; Debnath et al. 2020; Altaf et al. 2022d). In pepper plants, melatonin can even help counteract the toxic effects of arsenic (Kaya et al. 2022). These findings have important implications for the future of agriculture as we try to find more sustainable ways of growing crops. Tomato plants can benefit greatly from melatonin supplements, improving their ability for balancing minerals homeostasis (Jahan et al. 2021) and changing the structure of their roots in the face of cadmium toxicity (Altaf et al. 2022c). When exposed to acid rain, tomato seedlings gained notable benefits from being pre-treated with MEL, including better pigment content, secondary metabolites, and antioxidant enzyme activity while also mitigating MDA levels (Debnath et al. 2020). Li et al. (2022) also discovered that MEL can enhance the photosynthetic capacity and chlorophyll content of pepper seedlings under cold stress, as well as increase hormone metabolism and carotenoid content. These findings highlight the potential of melatonin to significantly improve crop health and productivity.

A recent study by Korkmaz et al. (2021) discovered that MEL was a significant contributor in enhancing the growth characteristics and gas exchange factors of peppers that were exposed to cold stress. The study also noted a reduction in H_2O_2 and MDA levels along with an increase in proline content and antioxidant enzymes. Another investigation conducted by Yakuboğlu et al. (2022) showed that the external application of MEL had a significant impact on the fresh and dry weight, pigment content, and antioxidant enzyme pool of potatoes under drought stress.

Melatonin is an essential regulator of photosystem I and II, and it upregulates the protein expression of these encoding genes in tobacco leaves when exposed to nitrogen dioxide, which is an air pollutant. It also helps to maintain the redox homeostasis and enhances the antioxidant defense system in plants according to Wang et al. (2022). There has been extensive research on the potential role of MEL in stress tolerance.

Melatonin has a variety of functions in plants, including growth, development, and stress response. More research is required to completely comprehend the processes by which melatonin acts in plants and its potential uses in agriculture and plant biotechnology. Knowing how melatonin functions in different plant growth phases can have a big impact on how well plants grow and produce, especially in challenging environmental conditions. The primary focus of this chapter will be on melatonin's function in plants and how it influences several growth stages, including seed germination, seedling growth and development, and yield related traits. The naturally occurring compound melatonin, which regulates circadian rhythms in animals, also plays a vital role in different plant processes such as growth, development, stress responses, and immune system function. With changing climate conditions and abiotic stresses affecting plant growth and yield, scientists are exploring new technologies and methods to minimize their impact and ensure high-quality, sustainable products. Melatonin has emerged as a potential plant hormone and key growth regulator that can help counteract the toxic effects of heavy metals and enhance plant growth characteristics, gas exchange factors, and antioxidant enzyme activity under stress conditions. Studies have shown that melatonin has the potential to significantly improve crop health and productivity and enhance stress tolerance in plants.

3.2 Melatonin Synthesis and Signaling Pathways in Plants

Melatonin (N-acetyl-5-methoxytryptamine) is an important signaling molecule in plants that plays a crucial role in regulating various physiological processes, including seed germination, growth and development, stress responses, and circadian rhythms (Hardeland et al. 2006). Melatonin is synthesized via the tryptophan pathway in plants, which involves a series of enzymatic reactions that convert tryptophan to serotonin and then to melatonin (Arnao and Hernández-Ruiz 2014).

The first step in the biosynthesis of melatonin in plants is the conversion of tryptophan to tryptamine, which is catalyzed by tryptophan decarboxylase (TDC) (Chen et al. 2009). TDC is a pyridoxal 5′-phosphate (PLP)-dependent enzyme that is encoded by multiple genes in plants. The second step involves the conversion of tryptamine to serotonin, which is catalyzed by serotonin N-acetyltransferase (SNAT) (Yeong Byeon et al. 2015). SNAT is a cytosolic enzyme that transfers an acetyl group from acetyl-CoA to the amino group of serotonin.

The final stage in the biosynthesis of melatonin in plants involves the conversion of serotonin to melatonin. This process is catalyzed by either serotonin N-methyltransferase (SNMT) or N-acetylserotonin O-methyltransferase (ASMT) (Hardeland et al. 2006). SNMT performs the transfer of a methyl group from S-adenosylmethionine (SAM) to the amino group of serotonin. In contrast, ASMT transfers an acetyl group from acetyl-CoA to the hydroxyl group of serotonin, leading to the formation of N-acetylserotonin (NAS). NAS is then methylated by SNMT to form melatonin.

Recent studies have shown that the biosynthesis of melatonin in plants is regulated by various factors, including light, temperature, and stress (Fan et al. 2018). Light is a key regulator of melatonin biosynthesis in plants, with blue and

UV-B light inducing the expression of TDC and SNAT genes while red and far-red light repressing their expression (Mannino et al. 2021). Temperature also plays a role in the regulation of melatonin biosynthesis in plants, with low temperature inducing the expression of SNMT and ASMT genes, leading to increased melatonin synthesis (Zhao et al. 2015).

Melatonin plays a crucial role in regulating plant growth and development, in addition to functioning as a potent antioxidant and scavenger of reactive oxygen species (ROS) that safeguards plants from oxidative stress (Ahmad et al. 2023). Furthermore, melatonin is involved in the modulation of genes that control stress responses, including heat shock proteins (HSPs), thereby improving plants' tolerance to both abiotic and biotic stress (Zeng et al. 2022). To summarize, the biosynthesis of melatonin in plants is a complex process that encompasses several enzymatic reactions and is regulated by various factors. Melatonin performs a crucial function in regulating plant growth and development, stress responses, and circadian rhythms, making it a promising candidate for enhancing plant productivity and stress tolerance in the fields of agriculture and horticulture.

3.2.1 Biosynthesis of Melatonin in Plants

The biosynthesis of melatonin in plants takes place through the tryptophan pathway, which involves several enzymes. Firstly, tryptophan is converted into serotonin by tryptophan decarboxylase (TDC). Subsequently, serotonin is transformed into N-acetylserotonin (NAS) by serotonin N-acetyltransferase (SNAT). Lastly, N-acetylserotonin O-methyltransferase (ASMT) converts NAS into melatonin (Murch and Erland 2021).

The biosynthesis of melatonin in plants is under the regulation of several environmental and developmental factors. For instance, studies have demonstrated that the production of melatonin in plants is triggered by abiotic stresses such as cold, heat, drought, and salinity (Zeng et al. 2022). Furthermore, the expression of genes involved in melatonin biosynthesis is regulated by the circadian clock, implying that melatonin synthesis may be regulated by the internal clock of the plant (Yang et al. 2022).

Melatonin has a wide range of functions in plants, including regulation of growth and development, improvement of stress tolerance, and acting as an antioxidant. Research has demonstrated that melatonin promotes seed germination, root growth, and lateral root formation (Yang et al. 2021). It has also been shown to enhance the ability of plants to tolerate various abiotic stresses, such as cold, heat, drought, and salinity (Zeng et al. 2022). Additionally, melatonin acts as an antioxidant, protecting plants from oxidative damage by scavenging free radicals (Tan et al. 2000).

The biosynthesis of melatonin in plants occurs via the tryptophan pathway and is regulated by environmental and developmental factors. Melatonin plays a variety of functional roles in plants, including regulating growth and development, enhancing stress tolerance, and acting as an antioxidant. Further research is needed to fully understand the mechanisms of melatonin biosynthesis and its functional roles in plants.

3.2.2 Melatonin Signaling Pathways

In plants, melatonin has been shown to regulate various processes, including seed germination, root growth, stress response, and secondary metabolism. The signaling pathways involved in melatonin-mediated processes in plants are not fully understood, but several studies have provided insights into the mechanisms by which melatonin functions in plants. One of the proposed signaling pathways involves the binding of melatonin to its receptors. In plants, two types of melatonin receptors have been identified: MT1 and MT2 (Boiko et al. 2022). These receptors are believed to be involved in regulating various physiological processes in plants, including growth and development, stress response, and circadian rhythms.

In addition to receptor-mediated signaling, melatonin may also modulate gene expression in plants. For example, in Arabidopsis thaliana, melatonin was found to upregulate the expression of genes involved in the biosynthesis of phenolic compounds, which are important for plant defense against pathogens and environmental stresses (Zeng et al. 2022). Melatonin may also interact with other signaling pathways in plants. For instance, melatonin was shown to interact with the abscisic acid (ABA) signaling pathway, which is involved in plant responses to abiotic stresses (Zeng et al. 2022). It was found that melatonin enhanced the expression of ABA-responsive genes, leading to increased tolerance to salt stress in rice (Tan et al. 2021).

Furthermore, melatonin has been shown to interact with reactive oxygen species (ROS) signaling pathways in plants. Under stress conditions, plants produce high levels of ROS, which can cause oxidative damage to cellular components. Melatonin has been shown to reduce ROS levels by upregulating the expression of antioxidant enzymes, such as superoxide dismutase (SOD) and catalase (CAT) (Qiu et al. 2019).

The signaling pathways involved in melatonin-mediated processes in plants are complex and multifaceted. While some progress has been made in understanding the mechanisms by which melatonin functions in plants, further research is needed to fully elucidate the signaling pathways involved.

3.2.3 Interaction of Melatonin with Other Plant Hormones

In plants, melatonin is known to interact with several plant hormones, such as auxins, cytokinins, gibberellins, ABA, and ethylene, to regulate diverse aspects of growth and development. These interactions emphasize the multifaceted role of melatonin and imply that it has crucial functions in coordinating the activities of different plant hormones. Auxins, a class of plant hormones, are involved in the regulation of plant growth and development, controlling cell division, elongation, and differentiation. Melatonin has been demonstrated to interact with auxins, influencing these processes. In Arabidopsis seedlings, melatonin has been shown to enhance the growth-promoting effects of auxins (Wang et al. 2016). Moreover, melatonin has been shown to promote lateral root formation in Arabidopsis via its interaction with auxins (Ren et al. 2019). These findings suggest that melatonin plays a role in coordinating the activities of auxins, providing insights into the multifaceted nature of melatonin's effects on plant growth and development.

Auxins are a group of plant hormones that regulate various aspects of plant growth and development, including cell division, elongation, and differentiation. Studies have shown that melatonin can interact with auxins to regulate these processes. For example, it has been shown that melatonin can enhance the growth-promoting effects of auxins in Arabidopsis seedlings (Wang et al. 2016). In addition, melatonin has been shown to promote lateral root formation in Arabidopsis through interaction with auxins (Ren et al. 2019).

Cytokinins are a group of plant hormones that promote cell division and differentiation. Studies have shown that melatonin can interact with cytokinins to regulate these processes. For example, it has been shown that melatonin can enhance the cytokinin-induced shoot regeneration in tobacco (Arnao and Hernández-Ruiz 2018). In addition, melatonin has been shown to promote the growth of axillary buds in tobacco through interaction with cytokinins (Yang et al. 2022).

Gibberellins are a group of plant hormones that promote stem elongation and seed germination. Studies have shown that melatonin can interact with gibberellins to regulate these processes. For example, it has been shown that melatonin can enhance the gibberellin-induced stem elongation in rice seedlings (Hwang and Back 2022). In addition, melatonin has been shown to promote seed germination in rice through interaction with gibberellins (Jensen et al. 2023).

Abscisic acid (ABA) is a plant hormone that plays important roles in regulating stress responses and seed dormancy. Studies have shown that melatonin can interact with ABA to regulate these processes. For example, it has been shown that melatonin can enhance the ABA-induced stomatal closure in Arabidopsis (Jensen et al. 2023). In addition, melatonin has been shown to promote seed germination in wheat under salt stress by interacting with ABA (Chen et al. 2021).

Ethylene is a plant hormone that regulates various aspects of plant growth and development, including fruit ripening and senescence. Studies have shown that melatonin can interact with ethylene to regulate these processes. For example, it has been shown that melatonin can delay the ripening of strawberry fruit through interaction with ethylene (Verde et al. 2022). In addition, melatonin has been shown to delay the senescence of rice leaves through interaction with ethylene (Lou et al. 2023). Further research is needed to fully understand the mechanisms underlying these interactions and their functional roles in plants.

3.3 Melatonin and Seed Germination

In plants, melatonin biosynthesis has been detected in various tissues, such as roots, leaves, flowers, and seeds (Arnao and Hernández-Ruiz 2006). The role of melatonin in plants has been studied extensively in recent years, and it has been found to play a key role in regulating many aspects of plant growth and development, including seed germination.

Melatonin has been shown to promote seed germination in a variety of plant species, including wheat, soybean, rice, tomato, and Arabidopsis thaliana (Wang et al. 2022; Yu et al. 2021; Arnao and Hernández-Ruiz 2014; Chen et al. 2009). The effect of melatonin on seed germination is dose-dependent, with low concentrations (10–100 nM) promoting germination, while higher concentrations (above 1 μM) inhibiting germination (Pelagio-Flores et al. 2012). The mechanism by which melatonin promotes seed germination is still not fully understood, but several hypotheses have been proposed.

One proposed mechanism is that melatonin acts as an antioxidant and reduces oxidative stress during seed germination. Seeds are known to be under oxidative stress during germination, due to the high metabolic activity required for germination, which generates reactive oxygen species (ROS). Melatonin has been shown to scavenge ROS and protect seeds from oxidative damage, thus promoting germination (Heshmati et al. 2021). In addition, melatonin has been shown to increase the activities of antioxidant enzymes, such as superoxide dismutase (SOD) and catalase (CAT), which also contribute to reducing oxidative stress during seed germination (Awan et al. 2023).

Another proposed mechanism by which melatonin promotes seed germination is through its interaction with plant hormones, particularly abscisic acid (ABA) and gibberellins (GAs). ABA is known to inhibit seed germination, while GAs promote germination. Melatonin has been shown to reduce ABA levels and increase GA levels, thus promoting germination (Chen et al. 2021). In addition, melatonin has been shown to regulate the expression of genes involved in ABA and GA signaling pathways, further contributing to its effect on seed germination (Wang et al. 2022).

Finally, melatonin has also been shown to interact with other signaling pathways involved in seed germination, such as the nitric oxide (NO) and hydrogen sulfide (H2S) signaling pathways. Both NO and H2S have been shown to promote seed germination, and melatonin has been shown to increase the production of these signaling molecules, thus promoting germination (Martinez-Lorente et al. 2022).

Melatonin has been shown to play a key role in regulating seed germination in a variety of plant species. Its effect on seed germination is dose-dependent, with low concentrations promoting germination and higher concentrations inhibiting germination. The mechanism by which melatonin promotes seed germination is multifaceted and involves several pathways, including antioxidant defense, hormone regulation, and signaling pathways. The understanding of the role of melatonin in seed germination is still evolving, and further research is needed to fully elucidate the mechanisms involved. Nonetheless, the potential applications of melatonin in agriculture, particularly in improving seed germination and seedling establishment, are promising and warrant further investigation.

3.3.1 Relationship Between Melatonin on Seed Germination

Seed germination is a critical process in plant development that is regulated by multiple factors, including environmental cues and plant hormones. Melatonin is a hormone produced in plants and animals that has been shown to have various physiological roles, including regulating plant growth, development, and stress responses. Recent studies have reported the positive effects of exogenous melatonin application on seed germination and seedling growth. This review aims to summarize the current literature on the effect of melatonin on seed germination.

Melatonin is a hormone that is produced by animals, plants, and microbes and plays an important role in regulating circadian rhythms and sleep-wake cycles in animals. Recent studies have shown that melatonin may also play a role in regulating seed germination in plants. In this review, we will examine the current state of research on the effect of melatonin on seed germination, including its potential mechanisms of action.

Several studies have shown that melatonin can positively affect seed germination in a variety of plant species. For example, Chen et al. (2021) found that treatment with melatonin increased the germination rate of cucumber seeds under salt stress conditions. Similarly, Arnao and Hernández-Ruiz (2014) reported that melatonin treatment improved the germination rate and seedling growth of tomato seeds under high-temperature stress.

Melatonin may also help improve seed germination by protecting seeds from oxidative stress. For example, Li et al. (2021) found that melatonin treatment reduced oxidative damage and increased germination rates in rice seeds exposed to high-temperature stress. Similarly, Ye et al. (2016) reported that melatonin treatment improved the germination rate and reduced oxidative damage in maize seeds under drought stress.

In addition to its role in protecting seeds from stress, melatonin may also directly promote seed germination. For example, Huangfu et al. (2021) found that treatment with melatonin increased the germination rate and seedling growth of rice seeds under normal growth conditions. Similarly, Korkmaz et al. (2021) reported that melatonin treatment improved the germination rate of pepper seeds.

The mechanisms by which melatonin affects seed germination are not yet fully understood, but several potential pathways have been proposed. For example, melatonin may act as an antioxidant, reducing oxidative stress and protecting seeds from damage (Han et al. 2017). Melatonin may also interact with other plant hormones, such as abscisic acid (ABA) and gibberellins (GAs), which are known to regulate seed germination (Zhang et al. 2014b). Finally, melatonin may affect the expression of genes involved in seed germination, such as those encoding enzymes involved in cell wall degradation and reserve mobilization (Arnao and Hernández-Ruiz 2014).

The current literature suggests that melatonin can positively affect seed germination in a variety of plant species, by protecting seeds from stress and potentially directly promoting germination. However, further research is needed to fully understand the mechanisms by which melatonin affects seed germination and to determine the optimal conditions for its use in agriculture.

3.3.2 Mechanisms of Melatonin-Mediated Seed Germination

Melatonin has been shown to affect seed germination in a variety of ways. For example, melatonin may promote seed germination by protecting seeds from stress, by directly promoting germination, or by interacting with other plant hormones that are known to regulate seed germination (Li et al. 2014; Huangfu et al. 2021). However, the precise mechanisms by which melatonin affects seed germination are not yet fully understood.

One proposed mechanism by which melatonin may promote seed germination is by regulating the balance between reactive oxygen species (ROS) and antioxidants in seeds. ROS play an important role in regulating seed germination, but excessive ROS levels can lead to oxidative damage and inhibit germination (Bailly 2004). Melatonin has been shown to act as an antioxidant, scavenging ROS and protecting seeds from oxidative damage (Tan et al. 2000). By regulating ROS levels, melatonin may promote seed germination by creating an optimal oxidative environment for germination.

Another proposed mechanism by which melatonin may promote seed germination is by interacting with other plant hormones that are known to regulate seed germination, such as abscisic acid (ABA) and gibberellins (GAs). ABA is a plant hormone that inhibits seed germination, while GAs promote seed germination (Finkelstein et al. 2002). Melatonin has been shown to interact with ABA and GAs in a variety of ways. For example, melatonin has been shown to reduce ABA levels in seeds and increase GA levels, leading to increased seed germination (Li et al. 2019). Additionally, melatonin has been shown to interact with the ABA and GA signaling pathways, leading to changes in gene expression that promote seed germination (Li et al. 2019).

Finally, melatonin may promote seed germination by affecting the expression of genes that are involved in seed germination. For example, melatonin has been shown to upregulate the expression of genes encoding enzymes involved in cell wall degradation and reserve mobilization, which are important processes for seed germination (Arnao and Hernández-Ruiz 2014). By regulating gene expression, melatonin may promote seed germination by creating an optimal molecular environment for germination.

Melatonin can promote seed germination in a variety of ways, including by regulating ROS levels, interacting with other plant hormones, and affecting gene expression. However, further research is needed to fully understand the mechanisms by which melatonin affects seed germination and to determine the optimal conditions for its use in agriculture.

Table 3.1 Effect of melatonin concentration on seed germination in different plant species

Plant species	Melatonin concentration	Results	References
Cotton	20 μM	Increased germination rate, germination potential and final fresh weight	Xiao et al. (2019)
Rice	100 μM	Increased length of the shoot and root, and improved the activity of antioxidant enzyme	Yu et al. (2022)
Mustard	0.1 μM	Stimulates root growth in young seedlings	Chen et al. (2009)
Cucumber	0.1–1 mM	Improved growth of seedlings and reduced their susceptibility to nitrate stress	Zhang et al. (2017b)
Maize	500 μM	Increased activity of antioxident enzymes and reduced the amount of oxidative damage	Muhammad et al. (2023)

3.3.3 Impact of Melatonin on Seedling Growth

Several studies have investigated the impact of melatonin on seedling growth in plants, with promising results. In a study by Yu et al. (2022), melatonin was found to promote seedling growth in rice by increasing the length of shoots and roots. The researchers also observed an increase in the activity of antioxidant enzymes, which suggests that melatonin may improve stress tolerance in plants. Similarly, Liang et al. (2015) found that melatonin treatment increased seedling growth and photosynthesis in tomato plants. The researchers observed an increase in the levels of chlorophyll and carotenoids, which are important pigments for photosynthesis. Melatonin treatment also increased the activity of antioxidant enzymes and reduced oxidative damage in the plants.

In a study by Muhammad et al. (2023), melatonin was found to promote activity of antioxident enzymes and reduced the amount of oxidative damage in maize plants. The researchers observed an increase in the length of shoots and roots, as well as an increase in the levels of antioxidant enzymes. Melatonin treatment also reduced the accumulation of sodium ions in the plants, which is a common symptom of salt stress. Other studies have investigated the impact of melatonin on seedling growth in other plant species, such as maize and soybean (Yu et al. 2021), with similar results. Melatonin treatment was found to promote seedling growth and improve stress tolerance in these plants.

Several studies have demonstrated the positive impact of melatonin on seedling growth in plants. Melatonin treatment has been found to increase shoot and root length, improve photosynthesis, enhance stress tolerance, and reduce oxidative damage. These findings suggest that melatonin may be a useful tool for promoting plant growth and improving crop yields in agriculture. Melatonin can have a positive effect on seed germination, with increased germination rates and percentages observed in several studies (Table 3.1). Additionally, some studies found that melatonin can improve seedling growth and increase root length. In particular, melatonin was found to improve germination under stress conditions such as salt stress and drought stress in some plant species. However, the concentration of melatonin used in these studies varied widely, ranging from 0.1 μM to 1000 μM, indicating that the optimal concentration for promoting seed germination may depend on the plant species and the specific experimental conditions (Table 3.1).

3.4 Melatonin and Plant Establishment

Melatonin is a multifunctional molecule that has been found to play important roles in plant growth, development, and stress defense. In recent years, several studies have investigated the impact of melatonin on plant establishment, with promising results. Melatonin treatment has been found to promote seed germination, enhance seedling growth, improve stress tolerance, and promote root growth. These findings suggest that melatonin may be a useful tool for promoting plant establishment and improving crop yields in agriculture. This chapter provides an overview of the current state of research on melatonin and plant establishment.

Melatonin promotes plant establishment through several mechanisms. One of the main mechanisms by which melatonin promotes seed germination is by regulating the activity of enzymes involved in the breakdown of stored nutrients in the seed, such as α-amylase and β-amylase (Zhang et al. 2017a). Melatonin has also been found to regulate the expression of genes involved in seed germination, such as LEA (late embryogenesis abundant) proteins and ABA (abscisic acid) biosynthesis genes. In addition, melatonin has been found to enhance the uptake and transport of nutrients, such as nitrogen and phosphorus, which are essential for seedling growth (Qiao et al. 2019).

Melatonin also promotes plant establishment by enhancing stress tolerance. Melatonin has been found to enhance the activity of antioxidant enzymes, such as superoxide dismutase, catalase, and peroxidase, which scavenge reactive oxygen species (ROS) and prevent oxidative damage (Khan et al. 2020). Melatonin has also been found to regulate the expression of genes involved in stress tolerance, such as heat shock proteins, dehydrin proteins, and osmoprotectant biosynthesis genes (Khan et al. 2022).

Melatonin has been found to promote plant establishment in a variety of plant species, including tomato, rice, maize, cucumber, turfgrass, and bermudagrass (Yu et al. 2021; Chen et al. 2021). In tomato plants, melatonin treatment has been found to promote seed germination and enhance seedling growth under salt stress. In rice plants, melatonin treatment has been found to enhance the growth and development of seedlings under drought stress. In maize plants, melatonin treatment has been found to improve embryo establishment under drought stress by regulating carbohydrate metabolism and glutathione synthesis. In cucumber plants, melatonin treatment has been found to enhance root growth and abiotic stress tolerance. In turfgrass plants, melatonin treatment has been found to enhance stress tolerance and promote growth. In bermudagrass plants, melatonin treatment has been found to enhance salt tolerance and promote growth.

The positive effects of melatonin on plant establishment suggest that it may be a useful tool for improving crop yields and agricultural production. Melatonin could be applied to seeds or soil to promote seed germination and seedling growth or sprayed on plant leaves to enhance stress tolerance and growth. Melatonin could also be used to improve plant establishment in degraded or contaminated soils, as well as in areas with extreme environmental conditions, such as drought, salinity, or high temperatures. In addition to its potential use in agriculture, melatonin may also have applications in forestry and landscaping, as well as in the restoration of degraded ecosystems. Melatonin could be applied to tree seedlings or forest floors to promote growth and survival, or to improve the health and resilience of urban trees and green spaces.

3.4.1 Role of Melatonin in Root Development

Root development is a complex process that involves various physiological and biochemical events. Roots are essential for plant growth and development, as they play a crucial role in nutrient uptake, water absorption, and anchorage. Melatonin, a hormone primarily associated with the regulation of circadian rhythms, has been found to have a significant impact on plant growth and development, including root development. This chapter aims to provide an overview of the role of melatonin in root development.

Melatonin biosynthesis in plants is a multi-step process involving tryptophan as the precursor molecule. The initial step involves the conversion of tryptophan to tryptamine by the enzyme tryptophan decarboxylase (TDC) (Mannino et al. 2021). Tryptamine is then converted to N-acetyltryptamine (NAT) by the enzyme tryptamine 5-hydroxylase (T5H). Finally, NAT is converted to melatonin by the enzyme N-acetylserotonin methyltransferase (ASMT) (Hernendez-Ruiz et al. 2004).

Melatonin has been found to have a significant impact on root development in various plant species. It has been shown to promote root growth in Arabidopsis thaliana (Chen et al. 2009), tomato (Wei et al. 2014), and rice (Liang et al. 2017). In addition, melatonin has been found to enhance lateral root formation in maize and promote adventitious root formation in cucumber (Zhang et al. 2014b).

Melatonin influences root development through various mechanisms, including regulation of cell division and elongation, modulation of hormone levels, and regulation of gene expression. Melatonin has been found to promote cell division in root tips of Arabidopsis (Chen et al. 2009) and rice (Tang et al. 2014) through the upregulation of genes involved in the cell cycle. Melatonin has also been shown to regulate the levels of other plant hormones such as auxin, cytokinin, and gibberellins, which are known to play a critical role in root development (Wei et al. 2014; Bian et al. 2021).

Melatonin has also been found to regulate the expression of genes involved in root development. In Arabidopsis, melatonin has been shown to upregulate the expression of genes involved in cell wall synthesis and modification, which play a critical role in root elongation (Chen et al. 2009). In addition, melatonin has been found to upregulate the expression of genes involved in auxin transport and signaling, which are known to play a crucial role in root development (Wei et al. 2014).

Melatonin plays a critical role in root development in various plant species. It promotes root growth, enhances lateral root formation, and promotes adventitious root formation. Melatonin influences root development through various mechanisms, including regulation of cell division and elongation, modulation of hormone levels, and regulation of gene expression. Further research is needed to elucidate the precise molecular mechanisms underlying the effects of melatonin on root development.

3.4.2 Influence of Melatonin on Shoot Growth

Melatonin has been reported to promote shoot growth in various plant species. For example, in rice (Oryza sativa), exogenous application of melatonin resulted in a significant increase in shoot length, number of tillers, and fresh weight (Li et al. 2017a). Similarly, in tomato (Solanum lycopersicum), melatonin application stimulated shoot growth and improved fruit yield (Shi et al. 2015). The positive effect of melatonin on shoot growth has also been demonstrated in other plant species, including Arabidopsis thaliana (Zhang et al. 2014b) and cucumber (Cucumis sativus) (Wang et al. 2016).

The promotion of shoot growth by melatonin is thought to be mediated through various mechanisms, including the regulation of hormone biosynthesis and signaling pathways. For example, in rice, melatonin has been shown to increase the biosynthesis of gibberellins (GAs), a class of plant hormones that promote shoot growth, through the upregulation of GA biosynthetic genes (Li et al. 2017b). In addition, melatonin has been shown to regulate auxin signaling, which is essential for shoot growth and development, by modulating the expression of auxin-related genes (Shi et al. 2015). Melatonin has also been reported to increase the expression of genes involved in cytokinin biosynthesis and signaling, which are known to promote shoot growth in plants (Wang et al. 2016).

In addition to the mechanisms discussed above, it is worth noting that melatonin also acts as an antioxidant and scavenger of reactive oxygen species (ROS) in plants. ROS can accumulate in plants under stress conditions, leading to oxidative damage and inhibition of growth and development (Zhang et al. 2014a). By scavenging ROS, melatonin can alleviate oxidative stress and enhance plant growth and development. Melatonin exerts its influence on shoot growth through various mechanisms, including the modulation of hormone biosynthesis and signaling pathways. The findings from various studies suggest that melatonin has the potential to be used as a growth regulator in agriculture to improve crop productivity.

3.4.3 Effect of Melatonin on Stress Tolerance During Plant Establishment

Plant establishment is a critical phase in the life cycle of plants, during which they are particularly vulnerable to environmental stresses. Melatonin, a versatile molecule with various functions in plants, has been shown to improve stress tolerance during plant establishment by regulating various physiological and molecular pathways. This chapter reviews the current knowledge on the effect of melatonin on stress tolerance during plant establishment.

Melatonin and stress tolerance during plant establishment: Melatonin has been reported to improve stress tolerance during plant establishment in various plant species. For example, in maize (*Zea mays*), exogenous application of melatonin significantly enhanced seed germination and seedling growth under salt stress conditions (Kołodziejczyk et al. 2016). Similarly, in wheat (*Triticum aestivum*), melatonin application increased seed germination and seedling growth under drought stress conditions (Wei et al. 2014). The positive effect of melatonin on stress tolerance during plant establishment has also been demonstrated in other plant species, including tomato (*Solanum lycopersicum*) (Li et al. 2014) and cucumber (*Cucumis sativus*) (Zhang et al. 2012).

Mechanisms underlying the effect of melatonin on stress tolerance during plant establishment: The improvement of stress tolerance during plant establishment by melatonin is thought to be mediated through various mechanisms, including the regulation of antioxidant systems, stress-responsive genes, and hormone signaling pathways. For example, melatonin has been shown to increase the activity of antioxidant enzymes, such as superoxide dismutase (SOD) and catalase (CAT), which can scavenge reactive oxygen species (ROS) and alleviate oxidative stress in plants (Wei et al. 2014). Melatonin has also been reported to regulate the expression of stress-responsive genes, such as DREB1A and DREB2A, which are involved in abiotic stress responses (Kołodziejczyk et al. 2016). In addition, melatonin can modulate hormone signaling pathways, such as abscisic acid (ABA) and gibberellins (GAs), which are crucial for stress responses during plant establishment (Li et al. 2014).

Melatonin is a multifaceted molecule that can improve stress tolerance during plant establishment by regulating various physiological and molecular pathways. The findings from various studies suggest that melatonin has the potential to be used as a stress-protectant agent in agriculture to enhance crop productivity under stressful conditions.

3.5 Melatonin and Vegetative Development

In recent years, several studies have investigated the effects of melatonin on various aspects of vegetative development, such as plant growth, morphology, and photosynthesis. This chapter reviews the current knowledge on the role of melatonin in vegetative development.

Melatonin and plant growth: Melatonin has been reported to promote plant growth in various plant species. For example, in Arabidopsis thaliana, exogenous application of melatonin increased shoot and root biomass, as well as leaf area (Liang et al. 2017). Similarly, in rice (*Oryza sativa*), melatonin application increased shoot and root length, as well as fresh weight (Yan et al. 2021). The positive effect of melatonin on plant growth has also been demonstrated in other plant species, including maize (*Zea mays*) (Shi et al. 2015) and cucumber (*Cucumis sativus*) (Wang et al. 2016).

Melatonin has also been shown to influence plant morphology. For instance, in tomato (*Solanum lycopersicum*), melatonin treatment induced changes in leaf shape and increased the number of lateral roots (Altaf et al. 2022d). In Arabidopsis thaliana, melatonin treatment led to an increase in leaf thickness and leaf mesophyll cell size (Liang et al. 2017). Melatonin has also been reported to affect plant architecture, such as stem length and branching, in rice (Varghese et al. 2019) and maize (Shi et al. 2015).

Melatonin and photosynthesis: Melatonin has been reported to enhance photosynthesis in various plant species. For example, in cucumber (*Cucumis sativus*), melatonin treatment increased photosynthetic rate, stomatal conductance, and transpiration rate (Wang et al. 2016). Similarly, in rice (*Oryza sativa*), melatonin application enhanced photosynthetic efficiency by increasing chlorophyll content and photosynthetic electron transport rate (Varghese et al. 2019). The positive effect of melatonin on photosynthesis has also been demonstrated in other plant species, including Arabidopsis thaliana (Liang et al. 2017) and maize (Shi et al. 2015).

Mechanisms underlying the effects of melatonin on vegetative development: The mechanisms underlying the effects of melatonin on vegetative development are complex and involve various physiological and molecular pathways. Melatonin has been shown to regulate plant growth and morphology by modulating hormone signaling pathways, such as auxin and cytokinin signaling (Shi et al. 2015). In addition, melatonin has been reported to enhance photosynthesis by regulating the expression of genes involved in chlorophyll biosynthesis and photosynthetic electron transport (Varghese et al. 2019). Melatonin plays an important role in vegetative development by regulating various physiological and molecular pathways. The findings from various studies suggest that melatonin has the potential to be used as a growth-promoting agent in agriculture to enhance crop productivity and quality.

3.5.1 Regulation of Melatonin in Vegetative Growth

Melatonin, a ubiquitous molecule in plants, plays a crucial role in regulating various physiological processes, including vegetative growth (Arnao and Hernández-Ruiz 2014). Several studies have demonstrated the beneficial effects of exogenous melatonin on the growth and development of different plant species (Li et al. 2014; Zuo et al. 2017). However, the underlying mechanisms of how melatonin regulates vegetative growth are not fully understood. Here, we summarize the recent advances in understanding the regulation of melatonin in vegetative growth.

Light is a critical environmental factor that regulates melatonin biosynthesis in plants. It has been reported that the biosynthesis of melatonin is stimulated by low-intensity blue light and inhibited by high-intensity white light (Murch et al. 2010; Lee et al. 2019). In Arabidopsis, the expression of TDC and SNAT is regulated by cryptochrome 1 (CRY1), a blue light photoreceptor (Hwang and

Back 2021). In addition, melatonin biosynthesis is also regulated by other environmental factors, such as temperature and nutrient availability. Moreover, endogenous factors, including hormones and transcription factors, can also modulate the expression of melatonin biosynthesis genes (Li et al. 2014; Hernández-Ruiz and Arnao 2008).

Melatonin has been shown to regulate various aspects of vegetative growth, including root development, shoot growth, and leaf senescence. Melatonin promotes root growth by regulating the expression of auxin biosynthesis and transport genes (Burkhardt et al. 2001; Tan et al. 2001). In addition, melatonin enhances shoot growth by increasing the activity of antioxidant enzymes and modulating the expression of genes involved in cytokinin signaling (Tan et al. 2002; Arnao and Hernández-Ruiz 2020). Furthermore, melatonin delays leaf senescence by modulating the expression of genes involved in hormone signaling and stress responses (Zhang et al. 2014a; Zhao et al. 2021).

Melatonin regulates vegetative growth by modulating various signaling pathways, including hormone signaling and stress responses (Li et al. 2014). Melatonin has been shown to interact with several hormones, including auxin, cytokinin, and abscisic acid (ABA), and modulate their signaling pathways (Byeon et al. 2015; Zhang et al. 2014b). For example, melatonin enhances the activity of auxin by regulating the expression of auxin biosynthesis and transport genes (Burkhardt et al. 2001; Tan et al. 2001). Similarly, melatonin enhances cytokinin signaling by modulating the expression of genes involved in cytokinin biosynthesis and signaling (Tan et al. 2002; Arnao and Hernández-Ruiz 2020). Moreover, melatonin also modulates the ABA signaling pathway by regulating the expression of genes involved in ABA biosynthesis and signaling (Zhang et al. 2019; Lee and Back 2016).

Melatonin also regulates stress responses by modulating the expression of stress-responsive genes (Chen and Arnao 2022). For example, melatonin enhances the tolerance of plants to various abiotic stresses, such as drought, salt, and heavy metal stress, by modulating the expression of genes involved in stress responses (Yin et al. 2013; Zhang et al. 2016). Furthermore, melatonin also enhances the resistance of plants to biotic stresses, such as pathogen infection, by modulating the expression of genes involved in defense responses (Zuo et al. 2017; Arnao and Hernández-Ruiz 2019).

Melatonin is a key regulator of vegetative growth in plants, and its biosynthesis, signaling, and transport are tightly regulated by various environmental and endogenous factors. The elucidation of these regulatory mechanisms will facilitate the development of strategies to enhance plant growth and productivity. However, further research is needed to fully understand the role of melatonin in vegetative growth and its potential applications in agriculture.

3.5.2 Interaction of Melatonin with Other Plant Hormones During Vegetative Development

Melatonin, as a pleiotropic molecule, has been shown to interact with various plant hormones during vegetative development, including auxins, cytokinins, gibberellins, abscisic acid, ethylene, and jasmonates. These interactions can have profound effects on plant growth and development, as well as stress responses. Here, we summarize the current understanding of the interactions between melatonin and other plant hormones during vegetative development.

Auxins are essential regulators of plant growth and development, and they play crucial roles in controlling cell division and elongation, organ formation, and tropic responses. Melatonin has been shown to interact with auxins in regulating various aspects of plant growth and development. For example, exogenous melatonin application has been found to promote adventitious root formation in cucumber seedlings by increasing the expression of auxin biosynthesis genes and enhancing auxin transport (Li et al. 2014). Similarly, melatonin treatment has been shown to stimulate primary root elongation in Arabidopsis by upregulating auxin-related genes (Chen et al. 2009). Melatonin has also been reported to increase the auxin content in maize seedlings, thereby promoting shoot growth.

Cytokinins are known to play important roles in controlling cell division and differentiation, shoot and root development, and stress responses. Melatonin has been shown to interact with cytokinins in regulating various aspects of plant growth and development. For example, melatonin has been found to enhance the cytokinin-induced greening of etiolated cucumber cotyledons, possibly by modulating the expression of cytokinin-related genes (Zhang et al. 2014b). In addition, melatonin treatment has been shown to increase the cytokinin content in Arabidopsis seedlings, which promotes shoot growth and enhances drought tolerance (Arnao and Hernández-Ruiz 2018).

Gibberellins are well-known plant hormones that promote stem elongation, seed germination, and floral induction. Melatonin has been shown to interact with gibberellins in regulating various aspects of plant growth and development. For example, melatonin has been found to promote stem elongation and increase the expression of gibberellin biosynthesis genes in pea seedlings (Kang et al. 2010). Melatonin has also been reported to enhance the effects of exogenous gibberellin application on the growth of Arabidopsis seedlings by upregulating gibberellin-related genes (Byeon et al. 2013).

Abscisic acid is a key hormone that regulates various aspects of plant growth and development, including seed germination, stomatal closure, and stress responses. Melatonin has been shown to interact with abscisic acid in regulating various aspects of plant growth and development. For example, melatonin treatment has been found to increase the expression of abscisic acid biosynthesis genes and promote stomatal closure in tomato plants (Kang et al. 2010). Melatonin has also been reported to enhance the effects of exogenous abscisic acid application on the drought tolerance of Arabidopsis seedlings by upregulating abscisic acid-related genes (Wei et al. 2014).

Ethylene is a gaseous hormone that plays important roles in regulating various aspects of plant growth and development, including fruit ripening, flower senescence, and stress responses. Melatonin has been shown to interact with ethylene in regulating various aspects of plant growth and development. For example, melatonin treatment has been found to reduce ethylene production and delay senescence in strawberry fruit (Shi et al. 2015). Melatonin has also been reported to enhance the effects of exogenous ethylene application on the growth of Arabidopsis seedlings by upregulating ethylene-related genes (Zhang et al. 2012).

Jasmonates are important plant hormones that play crucial roles in regulating various aspects of plant growth and development, including defense against herbivores and pathogens, root growth, and reproductive development. Melatonin has been shown to interact with jasmonates in regulating various aspects of plant growth and development. For example, melatonin treatment has been found to enhance the jasmonate-induced accumulation of anthocyanins in Arabidopsis seedlings, possibly by upregulating the expression of jasmonate biosynthesis genes (Zhang et al. 2014a). Melatonin has also been reported to enhance the effects of exogenous jasmonate application on the growth of rice seedlings by upregulating jasmonate-related genes (Shi et al. 2015).

Melatonin plays an important role in regulating various aspects of plant growth and development by interacting with other plant hormones, including auxins, cytokinins, gibberellins, abscisic acid, ethylene, and jasmonates. The interactions between melatonin and these hormones can have profound effects on plant growth and development, as well as stress responses. Further research is needed to elucidate the molecular mechanisms underlying these interactions and to develop strategies for utilizing these interactions to enhance plant growth and stress tolerance.

3.5.3 Effect of Melatonin on Plant Architecture

Plant architecture, including leaf morphology, stem length, and branching patterns, is an important determinant of crop yield and overall plant fitness. Recent studies have shown that the hormone melatonin plays a crucial role in regulating plant architecture by affecting various aspects of growth and development (Arnao and Hernández-Ruiz 2019). Melatonin is a highly conserved hormone that is synthesized in plants via the tryptophan pathway (Hardeland et al. 2011).

Melatonin has been shown to affect leaf morphology by regulating the size, shape, and number of leaves. In Arabidopsis, melatonin treatment increased leaf size and chlorophyll content (Zhao et al. 2015). In tomato plants, melatonin treatment increased leaf size and leaf area index (Zhang et al. 2014a). In rice, exogenous melatonin increased leaf length and width (Liang et al. 2015). These results suggest that melatonin may have a positive effect on leaf morphology and, ultimately, plant productivity.

Melatonin also plays a role in stem elongation and branching. In Arabidopsis, melatonin was found to promote stem elongation, leading to taller plants with longer internodes (Shi et al. 2015). In rice, exogenous melatonin treatment increased the

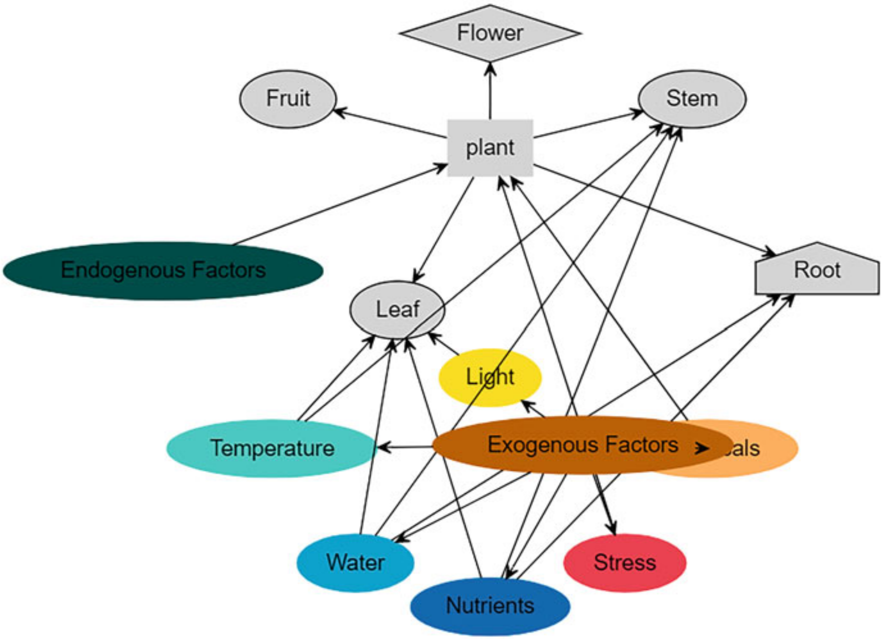

Fig. 3.1 The cluster graph showing clusters of plant parts and factors affecting melatonin production in plants. **Description of the diagram:** The "cluster_plant" subgraph contains five nodes that represent different parts of a plant: "root," "stem," "leaf," "flower," and "fruit." The "cluster_factors" subgraph contains seven nodes that represent different factors that can influence plant growth and productivity: "light," "temperature," "water," "nutrients," "stress," "chemicals," and "exogenous" (external) and "endogenous" (internal) factors. The edges in the graph show the relationships between the nodes. For example, there are edges connecting "light" to "leaf," "temperature" to both "stem" and "leaf," and "water" and "nutrients" to all three parts of the plant ("root," "stem," and "leaf"). There are also two edges that connect "stress" and "chemicals" to the "plant" node, which implies that these factors can have a broad impact on the plant as a whole. The graph provides a visual representation of the different factors that can affect plant growth and productivity and their relationships to different parts of the plant

number of tillers and the length of the main stem, resulting in plants with increased branching (Byeon et al. 2014). Melatonin may also affect branching by regulating the expression of genes involved in the biosynthesis of plant hormones such as auxin and cytokinin (Zhang et al. 2019).

Furthermore, melatonin has been shown to influence the development of flowers and fruits. In tomato plants, melatonin treatment increased the number of flowers per inflorescence and the number of fruits per plant (Li et al. 2014). In strawberries, exogenous melatonin treatment increased the number of flowers, resulting in increased fruit yield (Wang et al. 2016).

In conclusion, melatonin plays an important role in regulating plant architecture by affecting leaf morphology, stem elongation, branching, and fruit development (Fig. 3.1).

Further research is needed to elucidate the precise mechanisms by which melatonin regulates these processes.

3.6 Conclusion and Future Directions

The role of melatonin in the regulation of plant growth and development has gained significant attention in recent years. Melatonin is a multifunctional molecule that acts as a growth regulator, stress mitigator, and antioxidant in various plants. It has been found to play a crucial role in seed germination, plant establishment, and vegetative development by regulating several physiological processes, including root and shoot growth, photosynthesis, stomatal behavior, and hormonal balance. Melatonin acts as a growth promoter in seed germination and root development, while it suppresses shoot growth and promotes branching during vegetative development. Additionally, melatonin improves plant tolerance to various abiotic and biotic stresses during plant establishment, such as drought, salinity, and pathogen infections. Future studies could focus on understanding the molecular mechanisms underlying melatonin-mediated regulation of plant growth and development, including gene expression, signal transduction, and metabolite profiling. Additionally, the interactive effects of melatonin with other plant hormones could be investigated to understand their role in plant growth and development.

3.6.1 Summary of the Key Findings

The research on the role of melatonin in the regulation of plant growth and development has revealed several key findings. Firstly, melatonin has been found to play a significant role in seed germination, as it enhances the germination percentage and rate of various plant species. Secondly, melatonin has been shown to regulate root development by promoting primary root growth and lateral root formation. Thirdly, melatonin has been found to regulate shoot growth by suppressing stem elongation and promoting branching during vegetative development. In addition, melatonin has been found to improve plant tolerance to various abiotic and biotic stresses during plant establishment, such as drought, salinity, and pathogen infections. Melatonin acts as an antioxidant and stress mitigator, protecting plants from oxidative damage and improving their survival under stress conditions. Furthermore, melatonin has been found to interact with other plant hormones, such as auxins, cytokinins, and abscisic acid, to regulate plant growth and development.

3.6.2 Future Research Directions

Future research on the role of melatonin in the regulation of plant growth and development could focus on several areas. Firstly, understanding the molecular mechanisms underlying melatonin-mediated regulation of plant growth and development could provide insights into the gene expression, signal transduction, and metabolite profiling involved in this process. This could be achieved through techniques such as transcriptomics, proteomics, and metabolomics.

Secondly, further investigation of the interactive effects of melatonin with other plant hormones, such as auxins, cytokinins, and abscisic acid, could provide a better understanding of their role in regulating plant growth and development. This could involve studying the crosstalk between these hormones and melatonin, as well as their combined effects on different physiological processes.

Thirdly, the potential use of melatonin as a plant growth regulator and stress mitigator could be explored further. This could include investigating the effects of exogenous melatonin application on different plant species under different stress conditions, as well as optimizing the dose and timing of melatonin application.

Lastly, the potential use of melatonin in enhancing crop yield and improving plant stress tolerance could be investigated in field trials. This could involve studying the effects of melatonin on different crops under different environmental conditions, as well as developing strategies for the practical application of melatonin in agriculture.

In summary, future research on the role of melatonin in the regulation of plant growth and development could focus on understanding the molecular mechanisms underlying this process, investigating the interactive effects of melatonin with other plant hormones, exploring the potential use of melatonin as a plant growth regulator and stress mitigator, and investigating the potential use of melatonin in enhancing crop yield and improving plant stress tolerance in field trials.

References

Ahmad I, Song X, Ibrahim MEH, Jamal Y, Younas MU, Zhu G, Zhou G, Ali AYA (2023) The role of melatonin in plant growth and metabolism, and its interplay with nitric oxide and auxin in plants under different types of abiotic stress. Front Plant Sci 14(February):1108507. https://doi.org/10.3389/fpls.2023.1108507

Altaf MA, Shahid R, Ren M-X, Mora-Poblete F, Arnao MB, Naz S, Anwar M et al (2021) Phytomelatonin: an overview of the importance and mediating functions of melatonin against environmental stresses. Physiol Plant 172(2):820–846. https://doi.org/10.1111/ppl.13262

Altaf MA, Shu H, Hao Y, Zhou Y, Mumtaz MA, Wang Z (2022a) Vanadium toxicity induced changes in growth, antioxidant profiling, and vanadium uptake in pepper (capsicum annum L.) seedlings. Horticulturae 8(1):28. https://doi.org/10.3390/horticulturae8010028

Altaf MA, Shahid R, Altaf MM, Kumar R, Naz S, Kumar A, Alam P, Tiwari RK, Lal MK, Ahmad P (2022b) Melatonin: first-line soldier in tomato under abiotic stress current and future perspective. Plant Physiol Biochem 185(August):188–197. https://doi.org/10.1016/j.plaphy.2022.06.004

Altaf MA, Shahid R, Ren M-X, Naz S, Altaf MM, Khan LU, Lal MK, Tiwari RK, Shakoor A (2022c) Melatonin mitigates cadmium toxicity by promoting root architecture and mineral homeostasis of tomato genotypes. J Soil Sci Plant Nutr 22(1):1112–1128. https://doi.org/10.1007/s42729-021-00720-9

Altaf MA, Shahid R, Ren M-X, Naz S, Altaf MM, Khan LU, Tiwari RK et al (2022d) Melatonin improves drought stress tolerance of tomato by modulating plant growth, root architecture,

photosynthesis, and antioxidant defense system. Antioxidants 11(2):309. https://doi.org/10.3390/antiox11020309
Arnao MB, Hernández-Ruiz J (2006) The physiological function of melatonin in plants. Plant Signal Behav 1(3):89–95. https://doi.org/10.4161/psb.1.3.2640
Arnao MB, Hernández-Ruiz J (2014) Melatonin: plant growth regulator and/or biostimulator during stress? Trends Plant Sci 19(12):789–797. https://doi.org/10.1016/j.tplants.2014.07.006
Arnao MB, Hernández-Ruiz J (2018) Melatonin and its relationship to plant hormones. Ann Bot 121(2):195–207. https://doi.org/10.1093/aob/mcx114
Arnao MB, Hernández-Ruiz J (2019) Melatonin: a new plant hormone and/or a plant master regulator? Trends Plant Sci 24(1):38–48. https://doi.org/10.1016/j.tplants.2018.10.010
Arnao M, Hernández-Ruiz J (2020) Is Phytomelatonin a new plant hormone? Agronomy 10(1):95. https://doi.org/10.3390/agronomy10010095
Awan SA, Khan I, Wang Q, Gao J, Tan X, Yang F (2023) Pre-treatment of melatonin enhances the seed germination responses and physiological mechanisms of soybean (Glycine Max l.) under abiotic stresses. Frontiers in Plant Science 14:1149873. https://doi.org/10.3389/fpls.2023.1149873
Bailly C (2004) Active oxygen species and antioxidants in seed biology. Seed Sci Res 14(2): 93–107. https://doi.org/10.1079/ssr2004159
Bian L, Wang Y, Bai H, Li H, Zhang C, Chen J, Weimin X (2021) Melatonin-ROS signal module regulates plant lateral root development. Plant Signal Behav 16(5):1901447. https://doi.org/10.1080/15592324.2021.1901447
Boiko DI, Shkodina AD, Hasan MM, Bardhan M, Kazmi SK, Chopra H, Bhutra P, Baig AA, Skrypnikov AM (2022) Melatonergic receptors (Mt1/Mt2) as a potential additional target of novel drugs for depression. Neurochem Res 47(10):2909–2924. https://doi.org/10.1007/s11064-022-03646-5
Borges KL, Reis FW, Hippler R, Carvalho MEA, Nalin RS, Matias FI, Azevedo RA (2019) Nutritional status and root morphology of tomato under cd-induced stress: comparing contrasting genotypes for metal-tolerance. Sci Hortic 246(February):518–527. https://doi.org/10.1016/j.scienta.2018.11.023
Burkhardt S, Tan DX, Manchester LC, Hardeland R, Reiter RJ (2001) Detection and quantification of the antioxidant melatonin in Montmorency and Balaton tart cherries (*Prunus Cerasus*). J Agric Food Chem 49(10):4898–4902. https://doi.org/10.1021/jf010321+
Byeon Y, Lee HY, Lee K, Park S, Back K (2013) Cellular localization and kinetics of the rice melatonin biosynthetic enzymes SNAT and ASMT. J Pineal Res 56(1):107–114. https://doi.org/10.1111/jpi.12103
Byeon Y, Yool Lee H, Choi D-W, Back K (2014) Chloroplast-encoded serotonin N-acetyltransferase in the red alga Pyropia Yezoensis: gene transition to the nucleus from chloroplasts. J Exp Bot 66(3):709–717. https://doi.org/10.1093/jxb/eru357
Byeon Y, Choi G-H, Lee HY, Back K (2015) Melatonin biosynthesis requires *N*-Acetylserotonin methyltransferase activity of Caffeic acid *O*-methyltransferase in rice. J Exp Bot 66(21): 6917–6925. https://doi.org/10.1093/jxb/erv396
Chen Q, Arnao MB (2022) Phytomelatonin: an emerging new hormone in plants. J Exp Bot 73(17): 5773–5778. https://doi.org/10.1093/jxb/erac307
Chen Q, Qi W-b, Reiter RJ, Wei W, Wang B-m (2009) Exogenously applied melatonin stimulates root growth and raises endogenous Indoleacetic acid in roots of etiolated seedlings of brassica Juncea. J Plant Physiol 166(3):324–328. https://doi.org/10.1016/j.jplph.2008.06.002
Chen L, Bin L, Liu L, Duan W, Jiang D, Li J, Zhang K et al (2021) Melatonin promotes seed germination under salt stress by regulating ABA and GA3 in cotton (Gossypium Hirsutum L.). Plant Physiol Biochem 162(May):506–516. https://doi.org/10.1016/j.plaphy.2021.03.029
Debnath B, Li M, Liu S, Pan T, Ma C, Qiu D (2020) Melatonin-mediate acid rain stress tolerance mechanism through alteration of transcriptional factors and secondary metabolites gene expression in tomato. Ecotoxicol Environ Saf 200(September):110720. https://doi.org/10.1016/j.ecoenv.2020.110720

Fan J, Xie Y, Zhang Z, Chen L (2018) Melatonin: a multifunctional factor in plants. Int J Mol Sci 19(5):1528. https://doi.org/10.3390/ijms19051528

Finkelstein RR, Gampala SSL, Rock CD (2002) Abscisic acid signaling in seeds and seedlings. Plant Cell 14(suppl 1):S15–S45. https://doi.org/10.1105/tpc.010441

Francini A, Sebastiani L (2019) Abiotic stress effects on performance of horticultural crops. Horticulturae 5(4):67. https://doi.org/10.3390/horticulturae5040067

Han Q-H, Huang B, Ding C-B, Zhang Z-W, Chen Y-E, Hu C, Zhou L-J, Huang Y, Liao J-Q, Yuan S, Yuan M (2017) Effects of Melatonin on Anti-oxidative Systems and Photosystem II in Cold-Stressed Rice Seedlings. Front Plant Sci 8:785. https://doi.org/10.3389/fpls.2017.00785

Hardeland R, Pandi-Perumal SR, Cardinali DP (2006) Melatonin. Int J Biochem Cell Biol 38(3): 313–316. https://doi.org/10.1016/j.biocel.2005.08.020

Hardeland R, Madrid JA, Tan D-X, Reiter RJ (2011) Melatonin, the circadian multioscillator system and health: the need for detailed analyses of peripheral melatonin signaling. J Pineal Res 52(2):139–166. https://doi.org/10.1111/j.1600-079x.2011.00934.x

Hernández-Ruiz J, Arnao MB (2008) Distribution of melatonin in different zones of Lupin and barley plants at different ages in the presence and absence of light. J Agric Food Chem 56(22): 10567–10573. https://doi.org/10.1021/jf8022063

Hernendez-Ruiz J, Cano A, Arnao MB (2004) Melatonin: a growth-stimulating compound present in Lupin tissues. Planta 220(1):140–144. https://doi.org/10.1007/s00425-004-1317-3

Heshmati S, Dehaghi MA, Farooq M, Wojtyla Ł, Maleki K, Heshmati S (2021) Role of melatonin seed priming on antioxidant enzymes and biochemical responses of Carthamus Tinctorius L. under drought stress conditions. Plant Stress 2(December):100023. https://doi.org/10.1016/j.stress.2021.100023

Huangfu L, Zhang Z, Zhou Y, Zhang E, Chen R, Fang H, Li P et al (2021) Integrated physiological, metabolomic and transcriptomic analyses provide insights into the roles of exogenous melatonin in promoting rice seed germination under salt stress. Plant Growth Regul 95(1):19–31. https://doi.org/10.1007/s10725-021-00721-9

Hwang OJ, Back K (2021) Suppression of Rice Cryptochrome 1b decreases both melatonin and expression of Brassinosteroid biosynthetic genes resulting in salt tolerance. Molecules 26(4): 1075. https://doi.org/10.3390/molecules26041075

Hwang OJ, Back K (2022) Exogenous gibberellin treatment enhances melatonin synthesis for melatonin-enriched rice production. Biomol Ther 12(2):198. https://doi.org/10.3390/biom12020198

Jahan MS, Shu S, Yu W, Hasan M, El-Yazied AA, Alabdallah NM, Hajjar D, Altaf MA, Sun J, Guo S (2021) Melatonin pretreatment confers heat tolerance and repression of heat-induced senescence in tomato through the modulation of ABA- and GA-mediated pathways. Front Plant Sci 12(March):650955. https://doi.org/10.3389/fpls.2021.650955

Jensen NB, Ottosen C-O, Zhou R (2023) Exogenous melatonin alters stomatal regulation in tomato seedlings subjected to combined heat and drought stress through mechanisms distinct from ABA signaling. Plan Theory 12(5):1156. https://doi.org/10.3390/plants12051156

Kang K, Lee K, Park S, Kim YS, Back K (2010) Enhanced production of melatonin by ectopic overexpression of human serotonin N-acetyltransferase plays a role in cold resistance in transgenic rice seedlings. J Pineal Res 49:176. https://doi.org/10.1111/j.1600-079x.2010.00783.x

Kaya C, Sarıoglu A, Ashraf M, Alyemeni MN, Ahmad P (2022) The combined supplementation of melatonin and salicylic acid effectively detoxifies arsenic toxicity by modulating Phytochelatins and nitrogen metabolism in pepper plants. Environ Pollut 297(March):118727. https://doi.org/10.1016/j.envpol.2021.118727

Khan MN, Siddiqui MH, Mohammad F, Naeem M (2012) Interactive role of nitric oxide and calcium chloride in enhancing tolerance to salt stress. Nitric Oxide 27(4):210–218. https://doi.org/10.1016/j.niox.2012.07.005

Khan A, Numan M, Khan AL, Lee I-J, Imran M, Asaf S, Al-Harrasi A (2020) Melatonin: awakening the defense mechanisms during plant oxidative stress. Plan Theory 9(4):407. https://doi.org/10.3390/plants9040407

Khan A, Khan V, Pandey K, Sopory SK, Sanan-Mishra N (2022) Thermo-priming mediated cellular networks for abiotic stress management in plants. Front Plant Sci 13(May):866409. https://doi.org/10.3389/fpls.2022.866409

Kołodziejczyk I, Dzitko K, Szewczyk R, Posmyk MM (2016) Exogenous melatonin improves corn (Zea Mays L.) embryo proteome in seeds subjected to chilling stress. J Plant Physiol 193 (April):47–56. https://doi.org/10.1016/j.jplph.2016.01.012

Korkmaz A, Değer Ö, Szafrańska K, Köklü Ş, Karaca A, Yakupoğlu G, Kocaçinar F (2021) Melatonin effects in enhancing chilling stress tolerance of pepper. Sci Hortic 289 (November):110434. https://doi.org/10.1016/j.scienta.2021.110434

Krupa-Małkiewicz M, Fornal N (2018) Application of chitosan in vitro to minimize the adverse effects of salinity in petunia × Atkinsiana d. Don. Journal of Ecological Engineering 19(1): 143–149. https://doi.org/10.12911/22998993/79410

Lee HY, Back K (2016) Melatonin is required for H_2O_2- and NO-mediated defense signaling through MAPKKK3 and OXI1 in *Arabidopsis thaliana*. J Pineal Res 62(2):e12379. https://doi.org/10.1111/jpi.12379

Lee HY, Lee K, Back K (2019) Knockout of Arabidopsis serotonin N-Acetyltransferase-2 reduces melatonin levels and delays flowering. Biomol Ther 9(11):712. https://doi.org/10.3390/biom9110712

Li C, Tan D-X, Liang D, Chang C, Jia D, Ma F (2014) Melatonin mediates the regulation of ABA metabolism, free-radical scavenging, and stomatal behaviour in two malus species under drought stress. J Exp Bot 66(3):669–680. https://doi.org/10.1093/jxb/eru476

Li X, Bingjun Y, Cui Y, Yin Y (2017a) Melatonin application confers enhanced salt tolerance by regulating Na+ and Cl- accumulation in rice. Plant Growth Regul 83(3):441–454. https://doi.org/10.1007/s10725-017-0310-3

Li H, Chang J, Chen H, Wang Z, Xiurong G, Wei C, Zhang Y, Ma J, Yang J, Zhang X (2017b) Exogenous melatonin confers salt stress tolerance to watermelon by improving photosynthesis and redox homeostasis. Front Plant Sci 8(March):295. https://doi.org/10.3389/fpls.2017.00295

Li J, Zhao C, Zhang M, Yuan F, Chen M (2019) Exogenous melatonin improves seed germination in *Limonium bicolor* under salt stress. Plant Signal Behav 14(11):1659705. https://doi.org/10.1080/15592324.2019.1659705

Li R, Jiang M, Song Y, Zhang H (2021) Melatonin alleviates low-temperature stress via ABI5-mediated signals during seed germination in rice (Oryza Sativa l.). Frontiers in Plant Science 12: 727596. https://doi.org/10.3389/fpls.2021.727596

Li J, Ding D, Li N, Xie J, Jihua Y, Lyv J, Bakpa EP, Zhang J, Wang C, Zhang J (2022) Melatonin enhances the low-temperature combined low-light tolerance of pepper (capsicum Annuum L.) seedlings by regulating photosynthesis, carotenoid, and hormone metabolism. Environ Exp Bot 199(July):104868. https://doi.org/10.1016/j.envexpbot.2022.104868

Liang C, Zheng G, Li W, Wang Y, Bin H, Wang H, Hongkai W et al (2015) Melatonin delays leaf senescence and enhances salt stress tolerance in Rice. J Pineal Res 59(1):91–101. https://doi.org/10.1111/jpi.12243

Liang C, Li A, Yu H, Li W, Liang C, Guo S, Zhang R, Chu C (2017) Melatonin regulates root architecture by modulating auxin response in rice. Front Plant Sci 8(February):134. https://doi.org/10.3389/fpls.2017.00134

Lou J, Chenghao W, Wang H, Cao S, Wei Y, Chen Y, Jiang S, Shao X, Feng X (2023) Melatonin treatment delays postharvest senescence of broccoli with regulation of carotenoid metabolism. Food Chem 408(May):135185. https://doi.org/10.1016/j.foodchem.2022.135185

Mannino G, Pernici C, Serio G, Gentile C, Bertea CM (2021) Melatonin and Phytomelatonin: chemistry, biosynthesis, metabolism, distribution and bioactivity in plants and animals. An overview. Int J Mol Sci 22(18):9996. https://doi.org/10.3390/ijms22189996

Martinez-Lorente SE, Pardo-Hernadez M, Marti-Guillen JM, López-Delacalle M, Rivero RM (2022) Interaction between melatonin and NO: action mechanisms, Main targets and putative roles of the emerging molecule NOmela. Int J Mol Sci 23:6646. https://doi.org/10.20944/preprints202205.0279.v1

Muhammad I, Li Y, Shakeel A, Saqib F, Ahmad K, Nisar M, Saif U, Muhammad A, Shamsher A, Qing PL, Xun BZ (2023) Melatonin-priming enhances maize seedling drought tolerance by regulating the antioxidant defense system. Abs Plant Physiol 191(4) 2301-2315. https://doi.org/10.1093/plphys/kiad027

Murch SJ, Erland LAE (2021) A systematic review of melatonin in plants: an example of evolution of literature. Front Plant Sci 12(June):683047. https://doi.org/10.3389/fpls.2021.683047

Murch SJ, Hall BA, Le CH, Saxena PK (2010) Changes in the levels of Indoleamine phytochemicals during Véraison and ripening of wine grapes. J Pineal Res 49:95. https://doi.org/10.1111/j.1600-079x.2010.00774.x

Pelagio-Flores R, Muñoz-Parra E, Ortiz-Castro R, López-Bucio J (2012) Melatonin regulates Arabidopsis root system architecture likely acting independently of auxin signaling. J Pineal Res 53(3):279–288. https://doi.org/10.1111/j.1600-079x.2012.00996.x

Qiao Y, Yin L, Wang B, Ke Q, Deng X, Wang S (2019) Melatonin promotes plant growth by increasing nitrogen uptake and assimilation under nitrogen deficient condition in winter wheat. Plant Physiol Biochem 139(June):342–349. https://doi.org/10.1016/j.plaphy.2019.03.037

Qiu X, Wang X, Qiu J, Zhu Y, Liang T, Gao B, Zizhao W et al (2019) Melatonin rescued reactive oxygen species-impaired osteogenesis of human bone marrow mesenchymal stem cells in the presence of tumor necrosis factor-alpha. Stem Cells Int 2019(September):1–11. https://doi.org/10.1155/2019/6403967

Ren S, Rutto L, Katuuramu D (2019) Melatonin acts synergistically with auxin to promote lateral root development through fine tuning auxin transport in Arabidopsis Thaliana. PLoS One 14(8):e0221687. https://doi.org/10.1371/journal.pone.0221687

Rizhsky L, Liang H, Mittler R (2002) The combined effect of drought stress and heat shock on gene expression in tobacco. Plant Physiol 130(3):1143–1151. https://doi.org/10.1104/pp.006858

Sarafi E, Tsouvaltzis P, Chatzissavvidis C, Siomos A, Therios I (2017) Melatonin and resveratrol reverse the toxic effect of high boron (B) and modulate biochemical parameters in pepper plants (capsicum Annuum L.). Plant Physiol Biochem 112(March):173–182. https://doi.org/10.1016/j.plaphy.2016.12.018

Shi H, Qian Y, Tan D-X, Reiter RJ, He C (2015) Melatonin induces the transcripts of *CBF/DREB1s* and their involvement in both abiotic and biotic stresses in *Arabidopsis*. J Pineal Res 59(3):334–342. https://doi.org/10.1111/jpi.12262

Tan D-X, Manchester LC, Reiter RJ, Qi W-B, Karbownik M, Calvo JR (2000) Significance of melatonin in Antioxidative defense system: reactions and products. Neurosignals 9(3–4):137–159. https://doi.org/10.1159/000014635

Tan D-X, Manchester LC, Burkhardt S, Sainz RM, Mayo JC, Kohen R, Shohami E, Huo Y-S, Hardeland R, Reiter RJ (2001) N^1-acetyl-N^2-Formyl-5-Methoxykynuramine, a biogenic amine and melatonin metabolite, functions as a potent antioxidant. FASEB J 15(12):1–16. https://doi.org/10.1096/fj.01-0309fje

Tan D-X, Manchester LC, Hardeland R, Lopez-Burillo S, Mayo JC, Sainz RM, Reiter RJ (2002) Melatonin: a hormone, a tissue factor, an Autocoid, a Paracoid, and an antioxidant vitamin. J Pineal Res 34(1):75–78. https://doi.org/10.1034/j.1600-079x.2003.02111.x

Tan K, Zheng J, Liu C, Liu X, Liu X, Gao T, Song X, Wei Z, Ma F, Li C (2021) Heterologous expression of the melatonin-related gene HIOMT improves salt tolerance in malus Domestica. Int J Mol Sci 22(22):12425. https://doi.org/10.3390/ijms222212425

Tang Y, Cai B, Yuan F, He X, Lin X, Wang J, Wang Y, Yang G-Y (2014) Melatonin pretreatment improves the survival and function of transplanted mesenchymal stem cells after focal cerebral ischemia. Cell Transplant 23(10):1279–1291. https://doi.org/10.3727/096368913x667510

Tiwari RK, Lal MK, Naga KC, Kumar R, Chourasia KN, Subhash S, Kumar D, Sharma S (2020) Emerging roles of melatonin in mitigating abiotic and biotic stresses of horticultural crops. Sci Hortic 272(October):109592. https://doi.org/10.1016/j.scienta.2020.109592

Varghese N, Alyammahi O, Nasreddine S, Alhassani A, Gururani MA (2019) Melatonin positively influences the photosynthetic machinery and antioxidant system of Avena Sativa during salinity stress. Plan Theory 8(12):610. https://doi.org/10.3390/plants8120610

Verde A, Míguez JM, Gallardo M (2022) Role of melatonin in apple fruit during growth and ripening: possible interaction with ethylene. Plan Theory 11(5):688. https://doi.org/10.3390/plants11050688

Wang Q, An B, Wei Y, Reiter RJ, Shi H, Luo H, He C (2016) Melatonin regulates root meristem by repressing auxin synthesis and polar auxin transport in Arabidopsis. Front Plant Sci 07 (December):1882. https://doi.org/10.3389/fpls.2016.01882

Wang Y, Guo D, Wang J, Tian B, Li Y, Sun G, Zhang H (2022) Exogenous melatonin alleviates NO2 damage in tobacco leaves by promoting antioxidant defense, modulating redox homeostasis, and signal transduction. J Hazard Mater 424(February):127265. https://doi.org/10.1016/j.jhazmat.2021.127265

Wei W, Li Q-T, Chu Y-N, Reiter RJ, Xiao-Min Y, Zhu D-H, Zhang W-K et al (2014) Melatonin enhances plant growth and abiotic stress tolerance in soybean plants. J Exp Bot 66(3):695–707. https://doi.org/10.1093/jxb/eru392

Xiao S, Liantao L, Hao W, Dongxiao L, Zhiying B, Yongjiang Z, Hongchun S, Ke Z, Cundong L (2019) Exogenous melatonin accelerates seed germination in cotton (Gossypium hirsutum L.). PLOS ONE 14(6):e0216575. https://doi.org/10.1371/journal.pone.0216575

Yakuboğlu G, Ardıç ŞK, Cuci Y, Korkmaz A (2022) Mitigation of chilling stress effects on eggplant seedlings by exogenous application of melatonin. Turkish Journal of Agriculture - Food Science and Technology 10(4):562–568. https://doi.org/10.24925/turjaf.v10i4.562-568.4601

Yan F, Zhang J, Li W, Ding Y, Zhong Q, Xia X, Wei H, Li G (2021) Exogenous melatonin alleviates salt stress by improving leaf photosynthesis in rice seedlings. Plant Physiol Biochem 163(June):367–375. https://doi.org/10.1016/j.plaphy.2021.03.058

Yang L, Sun Q, Wang Y, Chan Z (2021) Global transcriptomic network of melatonin regulated root growth in Arabidopsis. Gene 764(January):145082. https://doi.org/10.1016/j.gene.2020.145082

Yang X, Chen J, Ma Y, Huang M, Qiu T, Bian H, Han N, Wang J (2022) Function, mechanism, and application of plant melatonin: an update with a focus on the cereal crop, barley (Hordeum Vulgare L.). Antioxidants 11(4):634. https://doi.org/10.3390/antiox11040634

Ye J, Wang S, Deng X, Yin L, Xiong B, Wang X (2016) Melatonin increased maize (Zea Mays L.) seedling drought tolerance by alleviating drought-induced photosynthetic inhibition and oxidative damage. Acta Physiol Plant 38(2). https://doi.org/10.1007/s11738-015-2045-y

Yin L, Wang P, Li M, Ke X, Li C, Liang D, Shan W et al (2013) Exogenous melatonin improves *Malus* resistance to Marssonina apple blotch. J Pineal Res 54(4):426–434. https://doi.org/10.1111/jpi.12038

Yu R, Zuo T, Diao P, Jiabin F, Fan Y, Wang Y, Zhao Q et al (2021) Melatonin enhances seed germination and seedling growth of Medicago Sativa under salinity via a putative melatonin receptor MsPMTR1. Front Plant Sci 12(August):702875. https://doi.org/10.3389/fpls.2021.702875

Yu Y, Liyuan Deng L, Zhou GC, Wang Y (2022) Exogenous melatonin activates antioxidant systems to increase the ability of rice seeds to germinate under high temperature conditions. Plan Theory 11(7):886. https://doi.org/10.3390/plants11070886

Zeng W, Mostafa S, Lu Z, Jin B (2022) Melatonin-mediated abiotic stress tolerance in plants. Front Plant Sci 13(May):847175. https://doi.org/10.3389/fpls.2022.847175

Zhang N, Zhao B, Zhang H-J, Weeda S, Yang C, Yang Z-C, Ren S, Guo Y-D (2012) Melatonin promotes water-stress tolerance, lateral root formation, and seed germination in cucumber (*Cucumis Sativus* L.). J Pineal Res 54(1):15–23. https://doi.org/10.1111/j.1600-079x.2012.01015.x

Zhang N, Sun Q, Zhang H, Cao Y, Weeda S, Ren S, Guo Y-D (2014a) Roles of melatonin in abiotic stress resistance in plants. J Exp Bot 66(3):647–656. https://doi.org/10.1093/jxb/eru336

Zhang H-J, Zhang N, Yang R-C, Wang L, Sun Q-Q, Li D-B, Cao Y-Y et al (2014b) Melatonin promotes seed germination under high salinity by regulating antioxidant systems, ABA and GA_4 interaction in cucumber (*Cucumis Sativus* L.). J Pineal Res 57(3):269–279. https://doi.org/10.1111/jpi.12167

Zhang N, Sun Q, Li H, Li X, Cao Y, Zhang H, Li S et al (2016) Melatonin improved anthocyanin accumulation by regulating gene expressions and resulted in high reactive oxygen species scavenging capacity in cabbage. Front Plant Sci 7(March):197. https://doi.org/10.3389/fpls.2016.00197

Zhang J, Shi Y, Zhang X, Hongmei D, Bin X, Huang B (2017a) Melatonin suppression of heat-induced leaf senescence involves changes in abscisic acid and Cytokinin biosynthesis and signaling pathways in perennial ryegrass (Lolium Perenne L.). Environ Exp Bot 138 (June):36–45. https://doi.org/10.1016/j.envexpbot.2017.02.012

Zhang R, Sun Y, Liu Z, Jin W, Sun Y (2017b) Effects of melatonin on seedling growth mineral nutrition and nitrogen metabolism in cucumber under nitrate stress Journal of Pineal Research 62(4) e12403. https://doi.org/10.1111/jpi.2017.62.issue-4

Zhang Q, Liu X, Zhang Z, Liu N, Li D, Longxing H (2019) Melatonin improved waterlogging tolerance in alfalfa (Medicago Sativa) by reprogramming polyamine and ethylene metabolism. Front Plant Sci 10(February):44. https://doi.org/10.3389/fpls.2019.00044

Zhao H, Lingfei X, Tao S, Jiang Y, Lingyu H, Ma F (2015) Melatonin regulates carbohydrate metabolism and defenses against *pseudomonas Syringae* Pv. *Tomato DC3000* infection in *Arabidopsis Thaliana*. J Pineal Res 59(1):109–119. https://doi.org/10.1111/jpi.12245

Zhao C, Guo H, Wang J, Wang Y, Zhang R (2021) Melatonin enhances drought tolerance by regulating leaf stomatal behavior, carbon and nitrogen metabolism, and related gene expression in maize plants. Front Plant Sci 12(December):779382. https://doi.org/10.3389/fpls.2021.779382

Zuo Z, Sun L, Wang T, Miao P, Zhu X, Liu S, Song F, Mao H, Li X (2017) Melatonin improves the photosynthetic carbon assimilation and antioxidant capacity in wheat exposed to Nano-ZnO stress. Molecules 22(10):1727. https://doi.org/10.3390/molecules22101727