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Role of melatonin on crop development: A review

Rol de la melatonina en el desarrollo de cultivos: una revisión

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ABSTRACT

Melatonin, a molecule initially discovered in animals, has gained increasing importance in recent decades due to its wide range of functions in the plant kingdom. This review examines the role of melatonin in crops, from its biosynthesis to its effects on various stages of plant development, including germination, vegetative growth, flowering, and senescence. Melatonin has been shown to act as a biostimulant in plants, enhancing germination, improving tolerance to abiotic stresses such as drought and salinity, and boosting both photosynthesis and biomass production. Recent studies have underscored its importance in regulating the circadian cycle and the plant's antioxidant response. Notable advances include research on high-value commercial crops, such as rice (*Oryza sativa* L.) and maize (*Zea mays* L.), where the exogenous application of melatonin has increased yield by 15% to 20% under stress conditions. The findings presented in this review highlight melatonin's potential, not only as a stress mitigator but also as a key component in the agronomic management of crops, enhancing productivity and sustainability in the face of current climate challenges. However, further research is needed to better understand its interactions with other phytohormones and its effectiveness across different agricultural species.

Keywords: abiotic stress; antioxidants; developmental stages; growth regulator; plant performance; plant physiology

RESUMEN

La melatonina, una molécula originalmente descubierta en animales, ha ganado relevancia en las últimas décadas debido a su amplia gama de funciones en el reino vegetal. Esta revisión analiza el papel que desempeña la melatonina en los cultivos, desde su síntesis hasta su impacto en diferentes etapas del desarrollo de las plantas, incluyendo la germinación, el crecimiento vegetativo, la floración y la senescencia. Se ha observado que la melatonina actúa como un bioestimulante en las plantas, mejorando la germinación, aumentando la tolerancia a estreses abióticos como la sequía y la salinidad, favoreciendo tanto la fotosíntesis como la producción de biomasa. Estudios recientes han resaltado su importancia en la regulación del ciclo circadiano y la respuesta antioxidante de las plantas. Entre los avances más destacados se encuentra la investigación sobre cultivos comerciales de alto valor como el arroz (*Oryza sativa* L.) y el maíz (*Zea mays* L.), donde la aplicación exógena de melatonina ha incrementado el rendimiento entre 15% y 20% bajo condiciones de estrés. Los hallazgos presentados en esta revisión resaltan el potencial de la melatonina, no solo como mitigadora del estrés, sino también como componente clave en la gestión agronómica de los cultivos para incrementar su productividad y sostenibilidad frente a los desafíos climáticos actuales. Sin embargo, se necesita más investigación para comprender mejor su interacción con otras fitohormonas y su eficiencia en diferentes especies agrícolas.

Palabras clave: antioxidantes; desempeño vegetal; estrés abiótico; etapas de desarrollo; fisiología vegetal; regulador del crecimiento

INTRODUCTION

Melatonin is a molecule initially identified for its role in regulating circadian rhythms in animals. However, research has also highlighted its significant involvement in plants. Although melatonin was first discovered in plants in 1995, it has since been recognized as an important regulator of various developmental processes and responses to environmental stressors (Arnao & Hernández-Ruiz, 2014). In plants, melatonin synthesis begins with the amino acid tryptophan, following a specific biochemical pathway that involves enzymes such as tryptophan decarboxylase (TDC), tryptamine 5-hydroxylase (T5H), and *N*-acetylserotonin methyltransferase (ASMT). These enzymes convert tryptophan into melatonin through several intermediates, including serotonin (Rodríguez, 2025).

Melatonin plays a prominent role throughout the various stages of plant development. During seed germination, its mitigates drought and salinity stress by protecting tissues from oxidative damage and promoting uniform and vigorous germination (Zhang *et al.*, 2022). At the vegetative growth stage, melatonin regulates the hormonal balance, particularly of auxins, which promote root development and leaf expansion, thereby increasing photosynthetic efficiency and nutrient uptake, both of which are crucial factors for plant development (Murch & Erland, 2021).

Additionally, during the reproductive stage, melatonin facilitates flowering and protects against adverse conditions such as cold and water deficit, which often delay these phase (Shi *et al.,* 2024). Studies have shown that plants treated with melatonin exhibit better synchronization of flowering and greater resistance to stressful conditions (Zhang *et al.*, 2022). Its antioxidant capacity is also crucial during the senescence phase, where it delays plant aging by reducing the accumulation of reactive oxygen species and protecting cells from oxidative damage (Arnao & Hernández-Ruiz, 2014).

The use of melatonin in agriculture has proven to be a promising strategy to enhance crop resilience against adverse environmental conditions, including drought, salinity, and low temperatures. Exogenous melatonin applications in crops such as rice, wheat, and tomato have led to significant yield increases, highlighting its potential as a biostimulant in sustainable agricultural systems (Liang *et al.*, 2017). These applications not only improve crop yield but also support sustainability in the face of current climate change challenges (Zhang *et al.,* 2014).

Reviews addressing the use of melatonin in mitigating biotic and abiotic stress, as well as its role across different phenological stages of plant development, remain scarce. For this reason, the objective of this review is to explore the use of melatonin in different phenological phases of plants and its physiological effect against various types of abiotic stress. Studies conducted on crops of agronomic interest are reviewed, highlighting how the exogenous application of melatonin can positively influence physiological and molecular processes that strengthen stress tolerance and improve crop productivity. Moreover, the potential of this molecule as a useful tool in the context of climate change is discussed, not only to mitigate its effects on agricultural production but also to guide new lines of research and more sustainable management strategies.

The methodology employed in this bibliographic review consisted of searching for relevant information, including scientific articles and book chapters, across various databases, following the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) guidelines. The key terms used in the search were "melatonin," "development stages," and "crops," which yielded 15,900 results from the past ten years (2014-2024) in the Google Scholar database (initially 35 publications were selected), 1,389 results in ScienceDirect (from which 21 were used), and 1,200 results in Semantic Scholar (five were selected).

In the final selection stage, articles and book chapters that appeared repeatedly across the different databases or did not explicitly address the effects of melatonin on the various developmental stages of crops were excluded. Special attention was given to publications focusing on crops of economic and agronomic importance, with particular emphasis on species cultivated in tropical and subtropical regions. Additionally, publications prior to 2014 were included when they were deemed to provide relevant information to the topic under study.

Melatonin

Melatonin (N-acetyl-5-methoxytryptamine) is a low-molecular-weight molecule that has been studied across various biological kingdoms. While in animals, especially mammals, it is well known for its role in regulating circadian rhythms and other physiological functions, its discovery in plants is relatively recent. Melatonin was first isolated and identified in 1958 by Lerner and his colleagues in bovine pineal gland tissue. It was not until 1995 that two researchers, Dubbels and Reiter, identified the presence of melatonin in plants, where its concentrations were found to be significantly higher than in vertebrates (Arnao & Hernández-Ruiz, 2014).

This molecule is highly conserved throughout evolution, suggesting its biological importance at a universal level. In plants, melatonin plays several essential roles, including functioning as an antioxidant that protects against oxidative damage caused by environmental stress (Reiter *et al.*, 2015). In addition, melatonin has been shown to stimulate plant growth and regulate various physiological processes, including seed germination, root development, photosynthesis, and flowering (Rodríguez, 2025).

It has been demonstrated that this molecule regulates plant growth and development by interacting with other plant hormones, such as abscisic acid and jasmonic acid; thereby modulating cell signaling, gene expression, and increasing stress tolerance. In particular, melatonin induces tolerance to heavy metals and enhances the phytoremediation capacity of plants by eliminating reactive oxygen species (ROS), thus playing a protective role in contaminated environments (Farouk & Al-Amri, 2019; Zhang *et al.*, 2022).

Regulation pathways of melatonin

In plants, melatonin is synthesized from the amino acid tryptophan, similar to its production in animals. This process occurs through four enzymatic steps (Ikram *et al.*, 2024):

Conversion of tryptophan to 5-hydroxytryptophan (5-HTP): The synthesis pathway begins with the conversion of tryptophan into 5-hydroxytryptophan (5-HTP), which can be catalyzed either by the enzyme tryptophan hydroxylase (TPH) located in the endoplasmic reticulum (ER) or by tryptophan decarboxylase (TDC) located in the cytoplasm. This step is crucial for the biosynthesis of melatonin, as well as other compounds such as serotonin (Arnao & Hernández-Ruiz, 2014).

Formation of serotonin: Next, 5-HTP is converted into serotonin by the action of L-aromatic amino acid decarboxylase. Serotonin is an essential intermediate in the melatonin biosynthetic pathway and also plays a role in the plant's response to stress (Shi *et al.*, 2024).

Conversion of serotonin to *N*-acetylserotonin: In the next step, serotonin is acetylated by the enzyme arylalkylamine *N*-acetyltransferase (AANAT) to form *N*-acetylserotonin. This critical step regulates the amount of melatonin produced and is influenced by environmental factors such as light and stress conditions (Liu *et al.*, 2022).

Formation of melatonin: The final step is the methylation of *N*-acetylserotonin by the enzyme hydroxyindole-O-methyltransferase (HIOMT), resulting in the production of melatonin. This process occurs in various plant tissues, including the leaves, stems, and roots, where melatonin plays several protective roles (Nawaz *et al.,* 2021).

The synthesis of melatonin in plants is strongly regulated by environmental factors (Liu *et al*., 2022). Stressors such as exposure to ultraviolet light, drought, cold, and excessive salinity activate melatonin biosynthetic pathways, leading to increased concentrations of melatonin and its precursors, such as tryptophan, tryptamine, and serotonin, in plant tissues. These increases help plants cope with adverse conditions and contribute to stress protection during aging (Ikram *et al*., 2024).

Melatonin as an abiotic stress mitigator

Abiotic stress refers to environmental conditions such as extreme temperature, drought, salinity, flooding, wind, and pollution, that negatively affect plant growth and development. The damage caused by these stressors depends on their duration and intensity and often leads to the generation of reactive oxygen species (ROS) (Espinoza & Reyna, 2019). The exogenous application of melatonin has proven to be an effective method for reducing the adverse effects of salt stress in plants. Additionally, increasing melatonin levels in various cellular compartments alters the content of the amino acid proline, a biochemical marker of stress (Dawood & El-Awadi, 2014). For this reason, melatonin has emerged as a defense enhancer, supporting plant adaptation by inducing the synthesis of endogenous melatonin and promoting the accumulation of metabolites (Zhang *et al*., 2022).

To counteract oxidative stress induced by abiotic factors, plants employ non-enzymatic antioxidant systems. These systems include flavonoids, phenolic compounds, and anthocyanins, which help neutralize free radicals and reduce their excessive production (Luo *et al.*, 2017). In addition, the modulation of these antioxidant compounds through the application of exogenous substances can influence the crop's ability to tolerate abiotic stress (Wu & Bose, 2024).

Melatonin activates both enzymatic mechanisms for ROS detoxification (such as SOD, CAT, POX, GR, and APX) and non-enzymatic mechanisms (ascorbic acid, carotenoids, and glutathione). At the cellular level, melatonin biosynthesis in plants is primarily associated with the chloroplasts and, to a lesser extent, the mitochondria. Under stress conditions, the expression of enzymes involved in its biosynthesis increases, resulting in reduced degradation of these organelles, which are typically associated with the production and accumulation of ROS (Wang *et al.*, 2022).

Other research has confirmed that melatonin also enhances tolerance to salt stress by regulating photosynthetic electron flow and the ascorbate-glutathione cycle in tomatoes (Yin *et al.*, 2019). In maize, the application of melatonin has been shown to increase drought tolerance by improving photosynthesis and reducing oxidative damage (Ye *et al.*, 2016). In maize seedlings, melatonin enhances salt tolerance by modulating the K^+/Na^+ balance (Verma *et al.,* 2020).

These properties make melatonin a promising tool for sustainable agriculture, especially in the context of climate change and increasing environmental pressures on crops (Ahmad *et al.,* 2023). This hormone not only enhances plant tolerance to abiotic stress but also plays a role in regulating critical physiological processes, including seed germination, photosynthesis, and root system architecture, further reinforcing its role in stress mitigation and promoting plant growth (Altaf *et al.,* 2023).

Functions of melatonin as a biotic stress mitigator

Modulation of the antioxidant defense system. Several studies have demonstrated that the exogenous application of melatonin enhances a plant's ability to cope with stress by increasing the activity of antioxidant systems. In studies conducted on maize (*Zea mays* L.) and cucumber (*Cucumis sativus* L.), it was shown that the application of melatonin under low temperature and high humidity stress conditions significantly reduced the levels of ROS, such as H_2O_2, and improved cell membrane integrity by decreasing peroxidase activity (Amin *et al.*, 2022; Li *et al.*, 2023).

Induction of defense genes and signaling pathways. Studies, like those by Shi *et al.* (2015), demonstrate that melatonin triggers the expression of various defense genes in plants, such as PR1, NPR1, CAT1, and SOD, which are directly involved in pathogen resistance and reducing oxidative stress. These genes strengthen natural defense barriers by activating salicylic acid (SA)-dependent signaling pathways. Additionally, melatonin activates the jasmonic acid (JA) signaling pathway, further boosting defense responses. These mechanisms have also been confirmed by Zhang *et al.* (2022), who found that melatonin stimulates both SA and JA pathways, enhancing plant immunity against a range of pathogens, including fungi and bacteria.

Strengthening of cell walls. Melatonin also plays a role in strengthening cell walls, which is crucial for preventing pathogen invasion. According to Pan *et al.* (2023), melatonin promotes the synthesis of lignin and callose, two compounds that reinforce cell walls and form physical barriers against pathogens. This finding is consistent with studies by Byeon *et al.* (2015), who found that melatonin helps prevent the penetration of fungi and bacteria by reinforcing cellular integrity.

Synergistic effect with other phytohormones. Melatonin does not function alone in defending against biotic stress. Arnao and Hernández-Ruiz (2015) suggest that melatonin interacts with other phytohormones, such as abscisic acid (ABA), which plays a key role in abiotic stress response contributes to biotic defense. Recent studies, such as that of Khan *et al.* (2024), have demonstrated that melatonin interacts with gibberellins and auxins to regulate the hormonal balance of plants, thereby optimizing their defensive responses against pathogens.

Contributions of melatonin in the phenological stages of plants

Breaking of dormancy. Seed dormancy constitutes a finely regulated physiological state that prevents germination under unfavorable environmental conditions, thereby ensuring species persistence through temporal control of germination (Finch & Leubner, 2006). In agricultural systems, the controlled release of dormancy is critical for achieving uniform germination, optimizing seedling establishment, and maximizing yield potential (Baskin & Baskin, 2014).

The application of melatonin in seed treatment is an emerging technique that promises to revolutionize agriculture, especially in crops with primary or secondary dormancy issues. Recalcitrant and orthodox seeds, primarily differentiated by their moisture content, may exhibit some form of dormancy that must be overcome to ensure efficient germination (Berjak & Pammenter, 2013; Baskin & Baskin, 2014). Primary dormancy is classified into three types: physiological, morphological, and morphophysiological. Physiological dormancy, the most prevalent form, involves hormonal regulation primarily through the ABA/GA ratio; dormancy is broken when GA levels increase or ABA is catabolized. Melatonin contributes to dormancy release by modulating this hormonal balance and enhancing germination (Shi *et al.*, 2015). Morphological dormancy arises from underdeveloped embryos, commonly in species requiring post-dispersal maturation. In such cases, melatonin facilitates embryo development, thereby accelerating dormancy alleviation (Li *et al.*, 2023).

Alternatively, morphophysiological dormancy is a combination of morphological and physiological barriers, further complicating germination. However, recent studies have shown that melatonin not only regulates hormonal balance in seeds with physiological dormancy but can also accelerate the maturation of morphologically dormant seeds, improving germination rates under various environmental conditions (Baskin & Baskin, 2014). These findings highlight the broad potential of melatonin to overcome different forms of dormancy, making its application in modern agriculture a promising alternative.

The interaction of melatonin with ABA and GA is essential to its role in seed germination. Melatonin reduces the concentration of ABA, a hormone that induces dormancy, while simultaneously promoting the synthesis of GA, which favors germination (Zhang *et al.*, 2023). This dual action allows melatonin to facilitate dormancy break and promote plant growth, highlighting its importance as a hormonal modulator in plant physiology.

Several studies have shown that melatonin can break seed dormancy and improve germination rates under various stress conditions. For example, in cereals such as wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.), the application of melatonin significantly reduces germination time and improves germination rates under both water and salt stress (Wei *et al.,* 2014). Specifically, in barley, melatonin application increased the germination rate by 20% under salt stress conditions, demonstrating its ability to break dormancy and enhance stress tolerance (Wei *et al.,* 2014).

Additionally, studies on cucumber have shown that melatonin not only improves germination under water stress conditions but also promotes lateral root formation, which is crucial for water and nutrient absorption (Zhang *et al*., 2023). In rice (*Oryza sativa* L.), melatonin has been shown to enhance germination and resistance to salt stress, increasing both seed viability and germination rates (Zeng *et al*., 2022). Similarly, in tomato (*Solanum lycopersicum* L.), melatonin has been found to improve germination and seedling growth under drought stress conditions (Luo *et al*., 2017).

Thus, the application of melatonin has proven to be an effective method for breaking seed dormancy in a wide range of crops, improving both germination rates and uniformity under various stress conditions. Experimental evidence supports its use in cereals such as wheat and barley, as well as in fruit crops like melon (C*ucumis melo* L.) (Burgueño, 2019).

Germination

Germination is a physiologically regulated process through which a seed transitions from dormancy to active metabolic function, initiating seedling development by mobilizing stored reserves (Adhikari *et al*., 2022). From an agronomic perspective, it encompasses coordinated biochemical and morphological changes that result in the emergence of a self-sustaining, photosynthetically competent seedling (Bewley *et al*., 2013). The efficiency and outcome of germination are modulated by environmental parameters including temperature, moisture, light, and nutrient availability, the optimization of which is crucial for maximizing germination performance and enhancing seedling vigor and nutritional quality (Baskin & Baskin, 2014).

This germination process is influenced by abiotic factors such as salinity, drought, and extreme temperatures, both high and low. In this regard, studies such as that reported by Gutiérrez (2021) indicate that the exogenous application of melatonin does not fully counteract the negative effects of salinity on germination; however, it does enhance the germination potential of pepper seeds. Similarly, Chen *et al*. (2020) report that under these stress conditions, melatonin improves the germination rate, speed, and percentage, although this effect largely depends on the species being sown.

Nevertheless, some authors have noted that under optimal conditions, the application of melatonin at high concentrations may delay the germination process. This response depends both on the applied dosage and the species, as the effect observed in one species at a given concentration may differ in another (Liu *et al.*, 2023).

Use of melatonin in seed priming

Melatonin has emerged as a key molecule in processes related to seeds, acting as a treatment that optimizes germination and prepares plants to withstand adverse conditions. Various studies have shown that the exogenous application of melatonin during priming can accelerate germination, enhance tolerance to abiotic and biotic stress, and promote the initial development of seedlings. This process holds significant importance for crops, particularly in regions affected by climate change and environmental stress, such as Latin America and the United States. In these regions, recent research has highlighted the benefits of melatonin priming in seeds of relevant agricultural species.

One of the primary benefits of melatonin in seed priming is the enhancement of germination. According to research by Arnao and Hernández-Ruiz (2014), melatonin enhances the activity of enzymes such as amylases, which break down starch reserves in seeds, facilitating their conversion into sugars that provide energy for initial growth. This step not only accelerates germination but also ensures greater uniformity in seedling development. Recent studies have shown that seed priming with melatonin application significantly improves germination rates and seedling vigor under thermal stress conditions in maize and tomato crops (Altaf *et al.*, 2023).

In addition to improving germination, melatonin also acts as a potent antioxidant, protecting seeds from oxidative stress caused by the accumulation of ROS during germination. Studies conducted in the United States, such as Tan *et al.* (2002), demonstrated that melatonin neutralizes ROS, reducing cellular damage and enhancing seedling viability. This antioxidant effect is further strengthened by the activation of antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT), as confirmed by the work of Back *et al.* (2016). Melatonin's ability to mitigate oxidative stress is especially relevant in regions affected by extreme climatic conditions, such as agricultural areas in Argentina, where water stress and high temperatures are recurring issues for crop germination (Huang & Jin, 2024).

Another relevant aspect of melatonin priming is its ability to regulate energy metabolism during germination. Liang *et al.* (2017) indicated that melatonin enhances mitochondrial efficiency, increasing ATP production and providing more energy for the metabolic processes that support seedling growth. This effect is particularly valuable in situations where seeds germinate under stressful conditions, as it enables seedlings to utilize energy resources more efficiently. Some studies have shown that melatonin reduces the accumulation of ROS during thermal stress, a critical factor in protecting cell membranes and maintaining nutrient uptake, photosynthetic efficiency, and other essential physiological processes under high-temperature conditions (Hassan *et al.*, 2022).

Similarly, melatonin interacts with other phytohormones that regulate seedling growth and defense. Studies conducted in Argentina have demonstrated that melatonin interacts with hormones such as abscisic acid (ABA) and jasmonic acid (JA) to regulate seed responses to adverse conditions. ABA, which predominates during dormancy, inhibits germination by maintaining low metabolic activity and protecting the seed from stress. JA, however, plays a crucial role in inducing the catabolism of ABA, thereby promoting the transition from dormancy to germination under favorable conditions. This hormonal balance enables seeds to respond optimally to environmental stimuli (Sano & Marion-Poll, 2021).

Additionally, in the United States, Back *et al*. (2016) observed that melatonin modulates auxin levels, promoting cell elongation and root development, which contribute to improved nutrient and water uptake during the early stages of growth. This hormonal interaction ensures a balance between growth and the activation of defense mechanisms, thereby preparing seedlings to better withstand environmental challenges.

Vegetative growth

Vegetative growth is a crucial stage in a plant's life cycle, during which it increases in size and mass, primarily through the development of roots, stems, and leaves. This process involves various phases, including cell division, elongation, and differentiation. Any form of stress encountered by the plant can delay growth and, consequently, reduce crop productivity (Ahmad *et al*., 2023).

Studies have reported that exogenous melatonin treatment stimulates cell division in both apical and lateral meristems, promoting stem and root elongation as well as the formation of new leaves. For instance, in a study by Azadshahraki *et al*. (2018), melatonin application in apple trees alleviated nutrient stress and increased the root-to-shoot ratio. Similarly, Burgueño (2019) demonstrated improvements in leaf number, stem length, leaf area, and dry weight in melon plants treated with melatonin. The 50 μM concentration produced the best results, primarily because melatonin promotes the development of longer and denser roots, thereby enhancing the plant's capacity to absorb water and nutrients.

Studies have also shown that seed germination benefits from the exogenous application of melatonin in crops such as wheat and rice under saline stress. This is attributed to melatonin's antioxidant properties and its ability to modulate metabolic pathways (Muhammad *et al*., 2024). These advantages extend to root development. For example, Ahmad *et al*. (2022) found that in corn seedlings, melatonin improved the root/shoot ratio, root length, and diameter, while also enhancing stem diameter and seedling height.

Reviews such as that by Sun *et al*. (2020) report that several studies have indicated that exogenous melatonin stimulates coleoptile growth in canary grass (*Phalaris canariensis* L.), wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), and oat (*Avena sativa* L.). It has also been shown to promote vegetative growth in agriculturally important species such as soybean (*Glycine max* (L.) Merr.), maize (*Zea mays* L.), and cucumber (*Cucumis sativus* L.). The use of melatonin has extended to crops like tomato (*Solanum lycopersicum* L.), where low concentrations (0.1 μmol) favored the formation of adventitious roots by inducing nitric oxide (NO) production. This compound influenced the expression of various auxin-related genes, including those involved in auxin transport, signal transduction, and hormone accumulation.

Furthermore, research conducted by Gutiérrez (2021) indicated that melatonin application can increase crop yield by promoting more vigorous growth and greater tolerance to salinity stress. This effect was particularly evident during the germination stage, where a 10 µM dose of melatonin resulted in the highest germination rates by the final day of evaluation. In contrast, a 100 µM dose showed no positive effect. The study also examined the effects of exogenous melatonin on *Capsicum* varieties under salinity stress, observing that a 50 µM dose increased seedling stem height. Plants not treated with melatonin showed limited salt tolerance, while those treated with increasing doses exhibited enhanced resistance and higher survival rates. These findings suggest that melatonin-treated plants generally produce more biomass, including increased leaf, stem, and root development.

Similarly, a study by Simlat *et al.* (2018) reported that melatonin can increase leaf number, promote bud growth, and enhance plant fresh weight. However, at high concentrations, melatonin acts as an inhibitor. Thus, it is evident that the exogenous application of melatonin supports plant growth and development, provided it is applied under optimal conditions to avoid adverse effects.

In crops exposed to drought stress, reduced gas exchange during photosynthesis is a common consequence. However, exogenous melatonin has been shown to improve carbon assimilation and increase the levels of photosynthetic pigments (Ahmad *et al.*, 2022).

In summary, melatonin plays a vital role in plant development by promoting germination, stimulating root growth, protecting against environmental stress, and improving photosynthetic efficiency—ultimately contributing to healthier and more sustainable plant growth.

Flowering

Melatonin plays a pivotal role in the regulation of flowering, functioning as a key signaling molecule in the control of plant developmental and photoperiodic responses (Fig. 1). Beyond its roles in seed germination and early seedling growth, melatonin has been implicated in the induction and development of floral structures, highlighting its broader involvement in plant reproductive processes. Research has demonstrated that melatonin interacts with phytochromes, key light receptors involved in controlling flowering in photoperiodic plants. In crops, melatonin has been found to slow down early flowering by regulating GA levels, delaying the floral transition, particularly under low-light conditions (Arnao & Hernández-Ruiz, 2018; Liang *et al.,* 2017). This finding is essential in situations where light conditions vary across seasons. In tomato plants, exogenous melatonin treatment extends the vegetative stage, reducing premature flowering and improving overall flower yield (Arnao & Hernández-Ruiz, 2020).

In crops such as soybean, it has been demonstrated that the application of melatonin under drought stress conditions helps maintain normal flowering. Melatonin stabilizes the plant's circadian cycle, which is essential for proper synchronization of flowering, even under adverse conditions (Chung & Deng, 2020). This function highlights the adaptogenic role of melatonin, integrating environmental and physiological signals that regulate the timing of flowering. Additionally, melatonin activates the expression of key genes involved in floral induction, such as FT (FLOWERING LOCUS T) and SOC1, which play a fundamental role in the transition from the vegetative to the reproductive stage (Yang *et al.*, 2022).

In sunflowers, the application of melatonin during the pre-flowering phase resulted in a higher number of flower heads and improved drought resistance, which enhanced pollen quality and seed viability (Ahmad *et al*., 2021). Such studies emphasize melatonin's ability to mitigate the impact of abiotic stress during critical stages of the plant's life cycle, such as flowering.

Fruit development and ripening

During the fruiting process, melatonin contributes in various ways. In fruit development, it stimulates cell division and the growth of young fruits, favoring their size and weight. Regarding fruit ripening, research conducted by Chung and Deng (2020) indicates that the exogenous application of melatonin delays the postharvest ripening process in bananas. However, this effect is concentration-depend, with treatments of 200 and 500 µM showing more effective results compared to the 50 µM treatment, which reduces ethylene production.

In tomato plants, research by Arnao and Hernández-Ruiz (2014) showed that tomatoes treated with 50 µM melatonin for 2 hours exhibited substantial changes in their fruit ripening parameters, including lycopene levels, fruit softening, taste, ethylene signaling, and biosynthetic enzyme activity, compared to untreated tomatoes. A similar effect was observed in stevia seedlings, where melatonin, depending on the doses, played a positive role in seedling development (Simlat *et al.,* 2018).

In the study conducted by Garrido (2021), it was noted that the application of melatonin in pomegranate increased yield, weight, sugar content, and bioactive compounds at the time of harvest. Similarly, it contributed to higher quality attributes after being stored for 3 months, as well as an increase in internal color due to the synthesis of anthocyanins in the fruit arils. This finding was also evidenced in "Lapins" cherries. Several studies have confirmed that preharvest melatonin application increases crop yield.

Melatonin has been linked to the modulation of gene expression at different developmental stages, including genes linked to flowering and ripening, which directly affects quality during fruit ripening. In addition, it influences the production of hormones such as ethylene, which is essential for ripening, and interacts with other phytohormones to fine-tune developmental responses. Its antioxidant properties also contribute to maintaining cellular integrity by reducing oxidative damage, thus promoting healthier fruit development and improving post-harvest quality (Himanshu *et al*., 2024).

In recent years, melatonin has attracted growing interest in postharvest research due to its potential as a sustainable strategy to extend fruit shelf life and mitigate chilling injury. As a tryptophan-derived molecule, it plays an important role in maintaining membrane stability and regulating cellular energy status. Its exogenous application has also been shown to modulate the biosynthesis of stress-related compounds, which enhances fruit tolerance to cold storage and reduces the physiological damage associated with low temperatures (Carrión-Antolí *et al.,* 2021; Carrión-Antolí *et al.,* 2022; Cortés-Montaña *et al.,* 2023).

Several studies have confirmed the positive effects of melatonin on the postharvest quality of different fruits. In crops such as peach (Wu *et al*., 2023), pear (Liu *et al.,* 2019), and mango (Bhardwaj *et al.,* 2021), the exogenous application of this phytohormone has been shown to enhance tolerance to low temperatures, reducing the incidence of physiological disorders associated with cold storage. Moreover, these treatments contributed to preserving key commercial attributes, including firmness, color, and bioactive composition, even after prolonged storage periods. Such evidence consolidates the role of melatonin as a promising strategy to extend fruit shelf life, with direct implications for the competitiveness and sustainability of agricultural production systems.

Exogenous applications of melatonin demonstrate the effects of melatonin on different fruit crops, showing that both the method of application—mainly by immersion—and the concentration used (expressed in micromolar or ppm) determine the physiological response of plants. In mangoes (*Mangifera indica* L.), for example, the application of 500 μM delayed fruit ripening and softening, while in bananas (*Musa acuminata* L.), concentrations of 200 and 500 μM prolonged the post-harvest ripening process. For applications in fruits such as apples—golden delicious (50 μmol L^{-1}) induced resistance to blue mold; in grapes, applications of 200 μM reduced berry abscission and rotten Index; immersion in bananas delayed chilling injury and alleviated peel browning. Taken together, the data suggest that melatonin acts by modulating ripening and other developmental processes in fruits, promoting better postharvest quality and contributing to extended shelf life (Himanshu *et al.*, 2024).

Senescence

Melatonin plays a fundamental role in plant senescence, a key process in the plant life cycle involving aging and programmed cell death of tissues. Several studies have shown how melatonin can delay this process through various mechanisms. First, its antioxidant capacity is crucial, as it reduces the levels of ROS, which accumulate during senescence and accelerate cellular deterioration. Acting as a potent free radical scavenger, melatonin protects plant cells from oxidative damage. This effect has been observed in crops such as cucumber and rice, where exogenous application has delayed cellular aging and improved root architecture by regulating genes related to auxin biosynthesis, such as AeYUCs and AeSAURs (Jing *et al.*, 2022).

Additionally, melatonin influences other phytohormones involved in the senescence process. For example, it interacts with ABA, a hormone that generally promotes senescence in plants. The application of melatonin has been shown to modulate the expression of genes involved in ABA metabolism (Fig. 1), thereby reducing its negative effects and extending the shelf life of horticultural products post-harvest (Azadshahraki *et al.*, 2018; Dong *et al.*, 2023). This delay in senescence is particularly evident in products such as broccoli and lettuce, where melatonin has been shown to be effective in prolonging their freshness and vitality (Luo *et al.,* 2017).

Melatonin also regulates senescence through interaction with other hormonal pathways, such as those of auxins. Recent studies has been shown that melatonin increases auxin levels in plants, which in turn inhibit the expression of senescence-related genes, such as SAG12, thereby promoting growth and delaying leaf aging (Zhang *et al.*, 2022). This mechanism has been tested in *Arabidopsis thaliana*, where the application of melatonin increased auxin biosynthesis and prolonged the shelf life of leaves post-harvest (Arnao & Hernández-Ruiz, 2014).

Table 1 presents several studies that highlight the effects of melatonin on various stages of plant development. This table emphasizes the role of melatonin in plant growth, influencing processes ranging from seed germination to senescence. It promotes root growth, delays flowering, regulates fruit ripening, and helps extend the lifespan of plant tissues. Additionally, melatonin significantly enhances plants' ability to tolerate various abiotic stresses, making it an essential molecule for supporting plant development under variable environmental conditions.

Table 1. *Effects of melatonin on various stages of plant development*

Development stage	Role of melatonin	Key insights	Authors
Seed germination	Enhances germination	Melatonin regulates seed germination by modulating redox balance and hormone signaling pathways, improving germination rates under stress conditions.	Pan *et al.* (2023); Ramasamy *et al.* (2023); Zhang *et al.* (2021).
Root development	Promotes root growth	Melatonin influences root morphology by stimulating root generation and enhancing root growth, similar to auxin-like activity.	Arnao and Hernández Ruiz (2018); Liu *et al.* (2022); Sun *et al.* (2020).
Flowering	Delays flowering	Melatonin stabilizes DELLA proteins and promotes FLC transcription, delaying flowering and inducing parthenocarpy.	Arnao and Hernández-Ruiz (2018); Arnao and Hernández-Ruiz (2020).
Fruit maturation	Regulates ripening	It promotes fruit ripening and delays senescence by regulating ethylene-related genes and enhancing antioxidant activity.	Arnao and Hernández-Ruiz (2018); Arnao and Hernández-Ruiz (2020); Sun *et al.* (2020).
Senescence	Delays aging	Melatonin preserves chlorophyll and protects photosynthetic systems, delaying leaf senescence and extending the lifespan of plant tissues.	Arnao and Hernández-Ruiz (2018); Sun *et al.* (2020); Zhang *et al.* (2021).
Stress response	Enhances tolerance	Melatonin improves tolerance to abiotic stresses like drought, salinity, and temperature by enhancing antioxidant defenses and modulating stress-related gene expression.	Pan *et al.* (2023); Sun *et al.* (2020); Wang *et al.* (2022).

These findings highlight the importance of regulating plant aging, offering new opportunities to improve the shelf life of crops and agricultural products through its application, both in enhancing yield and mitigating cellular aging.

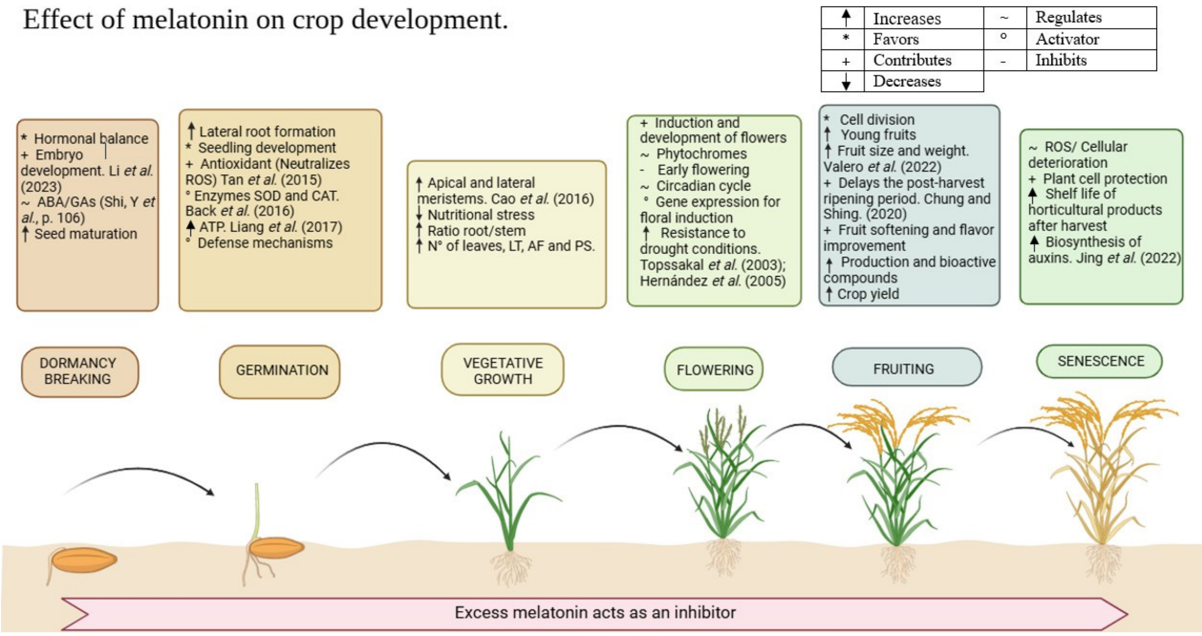

Figure 1. *Effect of melatonin on phenological stages*

CONCLUSIONS

The exogenous application of melatonin is a potent growth stimulant in various plant species, promoting cell division, stem and root elongation, and leaf formation, which significantly increases crop yield. However, its effectiveness depends on the concentration: optimal levels promote growth, while excessive concentrations act as inhibitors. Furthermore, melatonin helps plants adapt to changing environmental conditions and regulates flowering, although its effects may vary depending on the species and environmental factors. During fruiting, it stimulates fruit development, improves quality, and can delay both post-harvest maturation and senescence, thereby extending shelf life.

AUTHOR'S CONTRIBUTIONS

CLVG: Conceptualization, research, writing - original draft, visualization, writing, and editing; LFNH: Conceptualization, visualization, writing, and editing; ZCCR: Conceptualization, writing, and supervision editing; PJAM: Conceptualization, writing, and supervision editing. All authors have read and approved the final version of the manuscript.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest regarding the publication of this article.

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