Himanshu *et al.*
CABI Agriculture and Bioscience (2024) 5:103
https://doi.org/10.1186/s43170-024-00309-z

CABI Agriculture and Bioscience

REVIEW

Open Access

Unlocking the sustainable role of melatonin in fruit production and stress tolerance: a review

Himanshu[1†], Sunny Sharma[1*†], Vishal Singh Rana[1,2], Ankit[1], Vikanksha Thakur[1], Arun Kumar[1], Prachi[1], Shivender Thakur[1] and Neha Sharma[1]

Abstract

While melatonin, a vital player in plant physiology, initially attracted recognition due to its involvement in animal circadian rhythms, the molecule appears to be a multifunctional molecule requiring substantial attention for prospective applications in sustainable horticulture. It has been identified and recorded in numerous fruit crops, and its significance in physiological functions is critical for crop productivity. It is critical in safeguarding plants in response to reactive oxygen species in oxidative stress, one of the most damaging stressors to plant life in adverse conditions. Melatonin also cooperates with plants in boosting stress resistance, which concerns abiotic stress factors, e.g. low and high temperature, drought stress, toxicity of heavy metals, and biotic stress factors, including pests and pathogens. The anti-senescence properties of melatonin in aging leaves may be explained by its widespread antioxidant activity and its function in maintaining chlorophyll. The function of melatonin in controlling the production of genes linked to ethylene to modify postharvest fruit ripening has been the subject of an astounding amount of research. Additionally, recent research has shown that melatonin works with other phytohormones and well-known chemicals like nitric oxide and reactive oxygen species to assist plants in responding to biotic stress.The present review emphasizes a perspective that examining the role of melatonin in fruit crop physiology and stress responses may be a promising research direction in prospective fruit crop yield. In particular, this perspective is well supported by the following: melatonin is involved in the antioxidant response of fruit crops and can thus be used to mitigate the stressful impact of various environmental conditions; melatonin influences the development of plants and, consequently, affects fruit yield and quality; and applying melatonin is feasible for mitigating the impact of abiotic factors, such as cold, drought, heavy metals, and biotic factors, pests, and pathogens.

Introduction

According to Food and Agriculture Organization, to meet estimated food demands, there might be a one-third rise in the global population between now and 2050, so agricultural productivity will need to rise by 60% (Tyczewska et al. 2018). Production of fruit crops is crucial for several reasons, including cultural aspects, economic growth, environmental sustainability, and human nutrition. Fruits are an excellent means of fiber, antioxidants, vitamins, and minerals vital to human health (Omotayo and Aremu 2020). A variety of fruit intake can help people away from diseases and enhance general health. The production of fruit crops adds to dietary diversity by providing a diverse array of tastes, textures, and nutritional profiles. This diversity lowers the possibility of nutrient deficiencies by ensuring a diet that is both balanced and rich in nutrients. A substantial part of the agricultural sector, fruit production boosts both the local and national economies. Fruit sales and exports boost rural livelihoods, provide

[†]Himanshu and Sunny Sharma contributed equally to this work.

*Correspondence:
Sunny Sharma
sunny.29533@lpu.co.in
[1] School of Agriculture, Lovely Professional University, Phagwara, Punjab 144411, India
[2] Department of Fruit Science, Dr. Yashwant Singh Parmar University of Horticulture and Forestry, Solan, Himachal Pradesh, 173230, India

revenue for farmers, and increase the Gross domestic product (GDP) of the entire nation (Golovin et al. 2020). Particularly in rural areas, the production, harvesting, processing, and marketing of fruits creates job opportunities for a diverse workforce. Numerous nations participate in the international fruit trade. Fruit imports and exports support global trade by giving localities access to a wide range of fruits and enabling them to take part in the world economy (Cramer and Chisoro-Dube 2021). In many societies, fruits are symbolic and cultural objects. Some fruit trees also help to improve soil fertility and reduce soil erosion. Fruit orchards create tourists and support rural tourism, particularly those with beautiful surroundings. Certain fruit crops are resistant to environmental changes because they are suited to a particular climate (Gyawali et al. 2022. Research and innovation in fields like breeding, disease and pest management, and cultivation techniques are driven by the production of fruit crops. Technological developments support higher yields, better fruit quality, and sustainability. Sustainable methods of growing fruit, like agroforestry and organic farming, protect the environment, use fewer toxic chemicals, and improve soil health. Fruits support food security because they are a vital component of a balanced diet (Gamage et al. 2023).

Melatonin has a significantly smaller history in plants than it does in animals. Nevertheless, melatonin study in plants has advanced significantly in recent years. Melatonin can reduce oxidative stress and is specifically involved in many physiological processes in plants throughout the vegetative and reproductive phases. Melatonin's role in biological cycles and photoperiodic traits is also supported by evidence. Melatonin has the potential to regulate gene expression, growth, and development, protect plants from external biological stress, and facilitate interactions between plants and biotic factors (Agathokleous et al. 2019). It has been observed that melatonin, a hormone best known for controlling animal sleep–wake cycles, also has captivating functions in plants. In plants, melatonin functions as an efficient antioxidant that aids in the removal of reactive oxygen species (ROS). This is essential for shielding plant cells from environmental stressors like pollution, Ultravoilet (UV) rays, and other environmental factors that cause oxidative stress. Melatonin is a hormone that plants release in reaction to a variety of stresses, such as infections, severe weather, and drought (Ramasamy et al. 2023). Stressed plants have been found to have higher melatonin levels, which may play a part in their ability to adapt to harsh conditions. Plant defense mechanisms seem to involve melatonin. It can improve the expression of genes linked to pathogen defense, strengthening the plant's resistance to infection. Melatonin is believed to regulate plant growth and development and could influence seed germination, root growth, and flower development. Studies have shown that exogenous melatonin treatment affects key developmental processes (Ivanov et al. 2021). Melatonin may have an impact on how plants interact with other living things. It may be involved in the interactions between pollinators and plants as well as the attracting the beneficial insects. Furthermore, melatonin may impact both mutualistic and pathogenic relationships in plant–microbe interactions. It has been suggested that melatonin increases the vigor of seedlings (Cao et al. 2024).

Melatonin has a well-established role in plants as a plant growth regulator (PGR), impacting processes such as fruit set, seed germination, root proliferation, flowering, and ripening of fruits as shown in Table 1. Melatonin can also keep postharvest fruit fresher longer and increase its shelf life (Dai et al. 2020). Apart from its impact on these routine physiological functions, research has demonstrated that melatonin possesses antioxidant characteristics that are essential for eliminating reactive oxygen species (ROS) and reactive nitrogen species (RNS). It can offer resilience against many biotic and abiotic stressors, such as microbial infections (bacteria, viruses, and fungi), cold temperatures, salt, hot temperatures, and drought. Melatonin has been used to lessen the buildup of toxic metals and traces of pesticides in food (Tijero et al. 2019). Melatonin regulates growth and development and affects physiological processes essential for fruit output and quality. Studies imply its role in seed germination, flowering, fruit ripening, and post-harvest preservation. Melatonin may boost crop productivity and handle environmental changes by altering these mechanisms.

Plant resistance to abiotic and biological stresses has been enhanced by melatonin. Plants always produce melatonin in proportion to the degree of stress. In the same way, plants exhibit noticeably higher melatonin levels in response to a variety of stressors, such as salinity, drought, excessive watering, cold, high temperature, Ultraviolet radiation, and pollution (Zhang et al. 2022a, b). The transcription factors encoded by C-repeat binding factors (CBFs) and dehydration-responsive element-binding proteins (DREB) are crucial for many environmental stimuli, such as salt, drought, fungal infection, freezing, and cold stress. The expression of certain cold-responsive genes can be regulated by binding these CBF proteins to their promoter regions. In a similar vein, overexpressing AtCBF3, AtCBF2, and AtCBF1 increased resistance to freezing, salt, and drought by triggering several downstream genes, including those that are dehydration-responsive and cold-inducible. The defensive functions of melatonin and ABA in reaction to a variety

Table 1 Effect of melatonin on different fruit crops

Crop/crop species	Application method	Effective concentration (µM/ppm)	Plant response	References
Mangifera indica L.	Immersed	500 µM	Delayed ripening and softening	Liu et al. (2020)
Musa acuminata L.	Immersed	200 or 500 µM	Delayed postharvest ripening	Hu et al. (2017)
Kiwifruit	Immersed	50 µM	Enhanced their germination rate and germination potential	Shen et al. (2019)
Apple	Sprayed	–	Promoted adventitious root formation mainly at the stage of AR induction by increasing IAA levels and activating the function of MdWOX11 (overexpression lines)	Mao et al. (2020)
Grapes (5BB rootstock and the cultivar Cabernet Sauvignon)	Immersed	0.1 and 0.5 µM	Induced rooting in cultivar and rootstock	Gökbayrak et al. (2020)
Pomegranate	sprayed	5 ppm	Reduces the fruit drop and viable hermaphrodite flowers drop, which increases the fruit set	Usanmaz et al. (2022)
Apple	sprayed	20 and 200 µM	Improved flowering rate	Zhang et al. (2019a, b)
Apricot	sprayed	25 ppm	Increased vegetative growth	El-Naby et. (2019)
Sweet cherry	sprayed	0.3 mM	Improved crop yield and quality	Carrión-Antolí et al. (2021)
Pomegranate	sprayed	0.1 mM	Increased crop yield as well as fruit quality	Medina-Santamarina et al. (2021)
Grape (Kyoho)	Immersed	200 µM	Reduced berry abscission and rotten index	Wang et al. (2019)
Grape (Moldova)	Immersed	10 and 100 µM	Promoted berry ripening	Xu et al. (2018)
Banana	Immersed	–	Delayed chilling injury and alleviating peel browning	Cao et al. (2018)
Jujube	sprayed	200 µmol/L	Increased the disease resistance against *Alternaria rot*	Zhang et al. (2022a, b)
Apple (golden delicious)	Immersed	50 µmol/L	Induced resistance to blue mold	Wang et al. (2023)

of environmental stressors in different crops have been revealed with notable advancements in the last several years (Tiwari et al. 2021a, b).

The specific impact of melatonin on fruit production varies based on the species of the plant, the environment, and the methods of culture. Melatonin performs many roles in plant physiology and against various stresses (Ayyaz et al. 2022). Melatonin's role in seedling growth and germination has been explored and found that early development and ideal germination are two important elements that can influence total fruit production (Bulgari et al. 2019). For fruit set and pollination to be successful, flowering must occur at the appropriate time. Melatonin may affect the expression of genes involved in the formation of flowers. A possible role of melatonin in the ripening stages of fruit has been investigated in certain studies. The ripening genes' expression may be modulated by melatonin, which could impact the time and quality of fruit maturation (Arnao and Hernandez-Ruiz 2020). Antioxidant-rich melatonin has been shown to aid plants withstand environmental challenges. Melatonin may indirectly improve overall plant health and fruit output by lowering oxidative stress. Fruits' post-harvest qualities may be preserved by the antioxidant and anti-aging effects of melatonin (Khan et al. 2020). Despite these insights, there remains much to unravel regarding the intricate mechanisms underlying melatonin's actions in plants. Clarifying its signaling pathways, interactions with other phytohormones, and mode of action at the molecular level is critical for harnessing its full potential sustainably. In this review, we aim to consolidate current knowledge on melatonin's roles in fruit production and stress tolerance, highlighting its implications for sustainable agriculture. By elucidating its mechanisms and exploring practical applications, we can pave the way for innovative strategies to enhance crop resilience and yield in the face of escalating environmental challenges.

It has a significant effect on agriculture worldwide. It makes crops more resilient to environmental stressors such salinity, drought, and harsh temperatures, which can lead to much higher fruit yields and better quality fruits even in challenging circumstances. As a result, food supplies become more steady, promoting food security in the face of climate change. Additionally, melatonin usage promotes more environmentally friendly and sustainable farming methods by lowering the demand for chemical inputs like pesticides and fertilizers. These advantages help achieve the Sustainable Development Goals (SDGs) on a bigger scale, especially the ones that deal with ending hunger, responsible production and consumption, and climate action. In the end, melatonin integration into farming methods can improve food system sustainability, lessen environmental effects, and sustain farmers' livelihoods throughout the world.

Role sustainable development goal (SDGs)

The Sustainable Development Goals (SDGs) play a key role to advance science and its use in agriculture especially especially when it comes to strengthening the long-term benefits of melatonin for stress tolerance and fruit production. Plants naturally produce melatonin, which is well-known for its antioxidant qualities and capacity to improve crop stress tolerance Melatonin incorporation into agricultural operations is consistent with multiple SDGs, including Goals 2 (Zero Hunger), 12 (Responsible Consumption and Production), and 13 (Climate Action). By encouraging the incorporation of melatonin in fruit production, these SDGs promote sustainable agricultural techniques that boost crop productivity and resistance to environmental stressors such as drought and salinity. This strategy not only helps to ensure food security, but it also minimizes the need for artificial fertilizers and pesticides, promoting more sustainable consumption and production practices. Furthermore, improved crop resilience to climate-induced stresses is consistent with climate action programs, which help alleviate the effects of climate change on agriculture. Overall, the SDGs provide a framework for melatonin study and application in agriculture, promoting environmentally friendly techniques and global food systems.

Melatonin: an overview

Melatonin, also known as *N*-acetyl-5-methoxytryptamine, is a modified indoleamine that is generated from tryptophan and is extensively present in living, distantly related creatures (Juhnevica-Radenkova et al. 2020). In 1958, the isolation of this substance from the pineal gland of a cow. Melatonin has been considered to be an animal neurohormone for many years and its effects on seasonal reproductive cycles, mammalian immune system modulation, and circadian rhythm regulation are now old (Shao et al. 2024). Melatonin was also found in a variety of non-vertebrates in the 1980s. In 1989, it was discovered in a phototrophic unicell called *Gonyaulax polyedra* (now known as *Lingulodinium polyedrum*), and it was then thoroughly examined. Later, in 1995, it was discovered that certain plant species contained melatonin (Salehi et al. 2019).

Action mechanism of melatonin

The adaptable molecule melatonin, which is well known for its functions in animals, is equally essential to plants, especially when it comes to growth control and stress response. Melatonin's multipathway action mechanism in plants enables it to carry out a variety of tasks that promote plant development and resilience.

- Antioxidant activity: Melatonin functions as a strong antioxidant by scavenging reactive oxygen species (ROS) such hydrogen peroxide, hydroxyl radicals, and superoxide anions directly. This lessens oxidative stress, which is frequently brought on by a variety of abiotic stressors such as severe heat, salinity, and dehydration. Superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) are examples of antioxidant enzymes whose activity is increased by melatonin. By preserving cellular redox equilibrium, these enzymes further detoxify ROS (Tiwari et al. 2024).
- Gene expression regulation: Genes linked to stress tolerance are influenced by melatonin in their expression. As an example, it increases the expression of genes related to the manufacture of osmoprotectants, which aids in preserving osmotic equilibrium in stressful situations. Genes associated in plant growth, such as those governing root development, seed germination, and blooming, are expressed in a way that is regulated by melatonin. This modulation guarantees that even in less-than-ideal conditions, plants can maximize their growth (Gao et al. 2023). RNA-Seq was used to assess the genome-wide gene expression patterns of kiwifruit seedlings that had been primed with or without melatonin at 45 °C. Furthermore, qRT-PCR demonstrated that MT dramatically increased the expression of the carotenoid biosynthesis gene, which corresponded to an increase in carotenoid content. Furthermore, MT significantly increased the expression of 10 heat shock proteins (HSPs) (Xia et al. 2021).
- Signal transduction pathways: Melatonin is a signaling substance that initiates many pathways related to the stress response. It triggers signaling cascades of Mitogen-Activated Protein Kinase (MAPK), which are essential for delivering stress messages and starting the right kinds of cellular reactions. It regulates growth and stress responses by interacting with gibberellins, auxins, and abscisic acid, among other plant hormones. Crosstalk adjusts how plants react to external stimuli (Khalil et al. 2023).
- Photosynthesis and chloroplast function: Under stressful circumstances, melatonin prevents chlorophyll from degrading, preserving photosynthetic activity. For plants to produce energy and be healthy

overall, this is essential. By increasing light absorption and energy transfer inside the chloroplasts, melatonin raises the efficiency of photosystems I and II. Better growth and productivity result from this, even in challenging circumstances (Hussain et al. 2024).

- Root system architecture: Melatonin increases the elongation and development of lateral roots, which enhances a plant's capacity to absorb nutrients and water, particularly during droughts. It has an impact on the root microbiome as well, encouraging the development of advantageous microbes that improve stress tolerance and nutrient absorption (Wang et al. 2022a, b).
- Molecular and epigenic modifications: Melatonin has the ability to cause epigenetic modifications, such as histone modification and DNA methylation, which affect the patterns of gene expression and provide long-term stress tolerance. In addition, melatonin affects how proteins are modified post-translationally, such as via phosphorylation, which modifies the function of important enzymes and proteins involved in stress reactions (Kaya and Ugurlar 2023).

The ways that various organisms synthesize melatonin have varied over billions of years of evolution. Plants can create more melatonin than animals, and in general, their synthesis of the hormone is more sophisticated. The study employed isotope tracer technology to provide exogenous C14-labelled tryptophan. Ultimately, radioactive tryptamine, 5-hydroxytryptophan, indoleacetic acid, and melatonin were found in Hypericum monogynum (Wu et al. 2021a, b). The production of phytomelatonin involves four sequential enzymatic processes, the majority of which are catalyzed by five different enzymes (Mannino et al. 2021). The most crucial stage in the synthesis of melatonin is the alteration of tryptamine to serotonin, which is catalyzed by tryptophan decarboxylase (TDC) in the first two steps (Liu et al. 2022) as shown in Figs. 1 and 2. Afterward, tryptamine is converted to tryptamine by tryptamine-5-hydroxylase (T5H). Plants have two separate routes that lead from serotonin to melatonin in the following two phases (Erland et al. 2017). One pathway uses serotonin-*N*-acetyltransferase (SNAT) to catalyze the conversion of serotonin to *N*-acetylserotonin. Then, *N*-acetylserotonin methyltransferase (ASMT; formerly

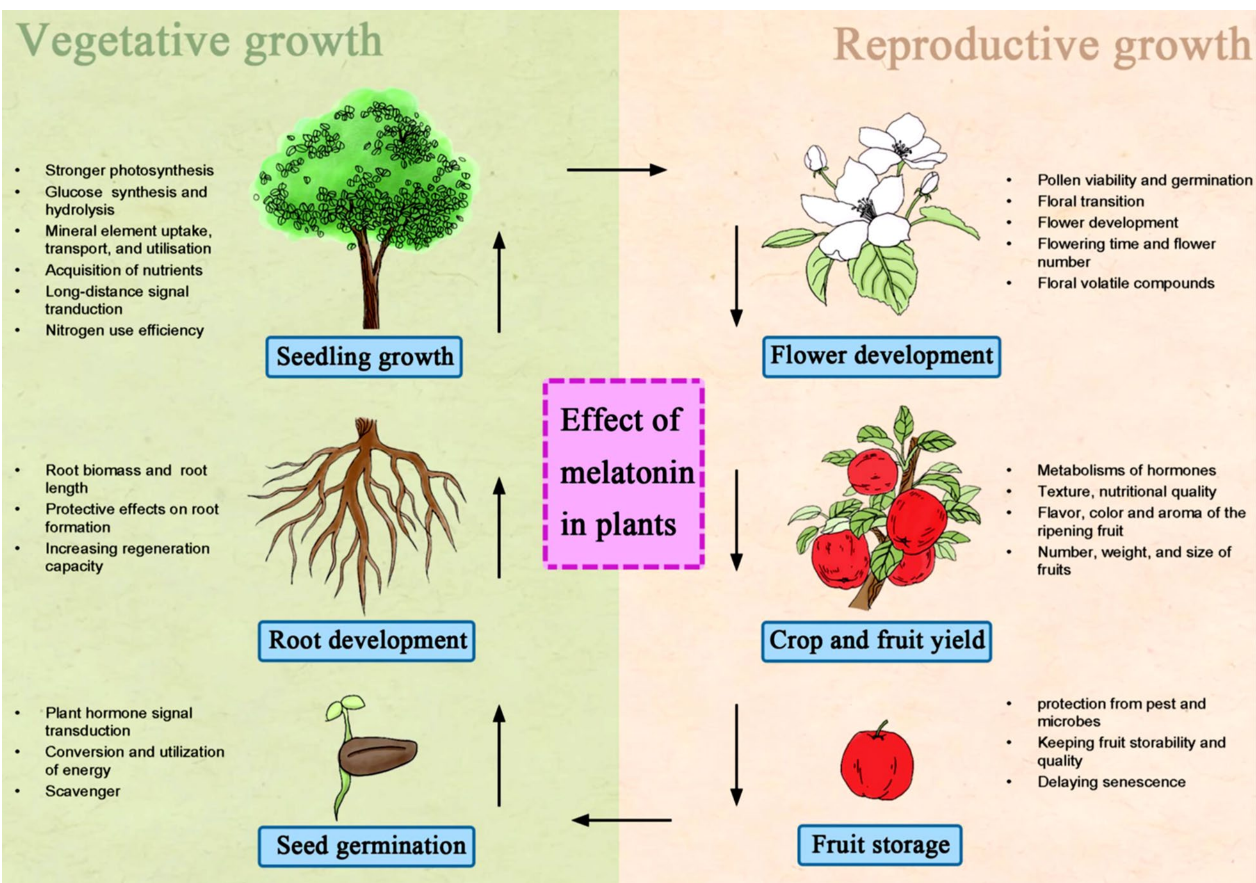

Fig. 1 Role of melatonin application in fruit crops (Pan et al. 2023)

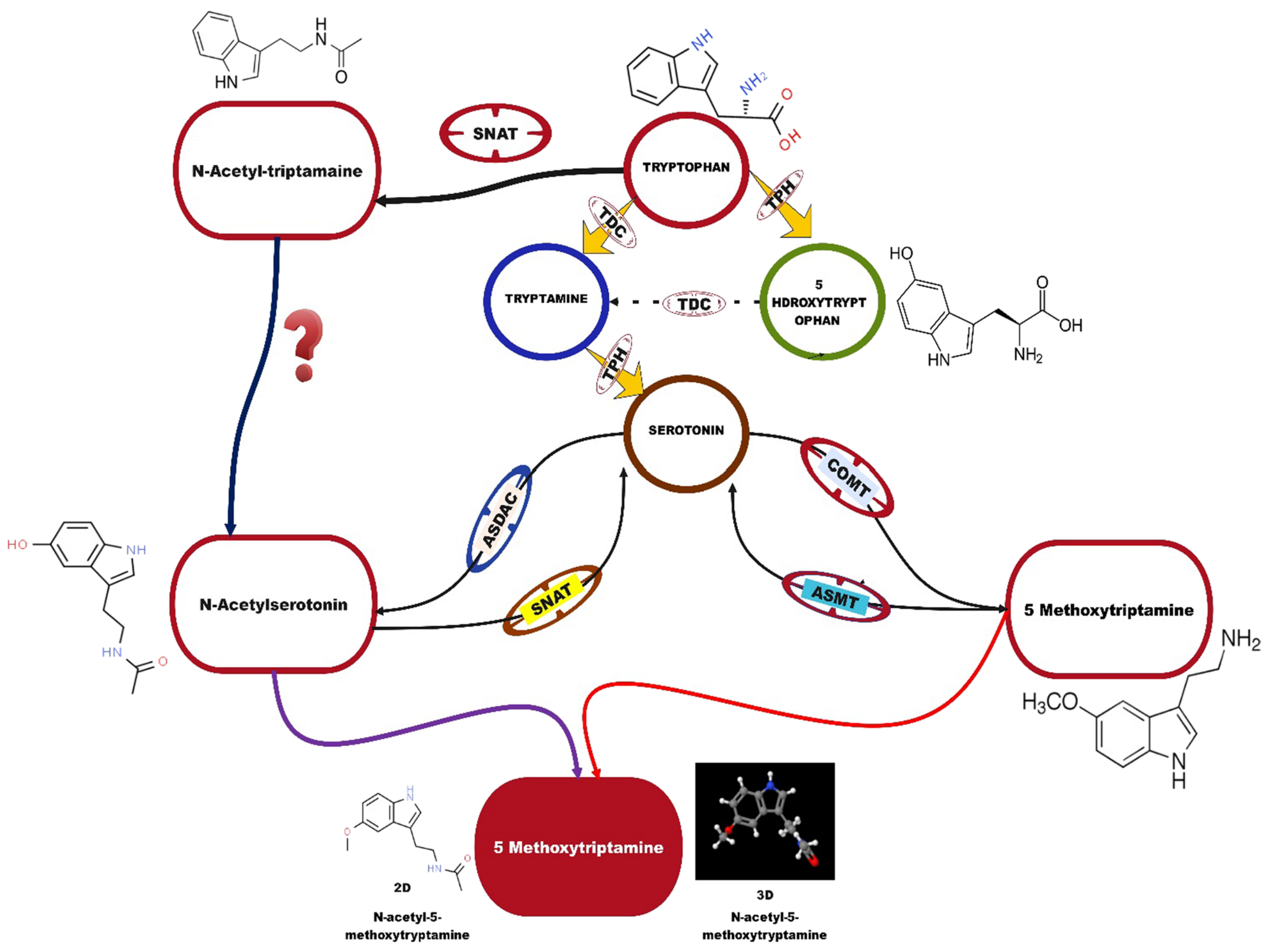

Fig. 2 Biosynthesis pathways of melatonin

known as hydroxyindole-*O*-methyltransferase, HIOMT) or caffeic acid *O*-methyltransferase (COMT) catalyzes the conversion of *N*-acetylserotonin to melatonin (Sharma et al. 2023). The second route, which is catalyzed by ASMT/COMT and SNAT, goes from serotonin to 5-methoxytryptamine and subsequently to melatonin. To further investigate the melatonin biosynthesis route in plants, a range of transgenic plants for melatonin synthesis have been created, and all the essential synthesis enzyme-coding genes have been cloned in plants thus far (Mir et al. 2020).

Different subcellular sites, including the cytoplasm, endoplasmic reticulum, and chloroplasts, generate melatonin intermediates. The cytoplasm may be the ultimate subcellular site of melatonin synthesis, depending on the pathway (Tan and Reiter 2020). This could have a different impact on the way that melatonin acts in plants. Both mitochondria and chloroplasts contain SNAT. These melatonin synthesis enzyme subcellular locations imply that melatonin production sites expanded during evolution to include the cytoplasm and endoplasmic reticulum, becoming more diversified (Suresh et al. 2023).

Melatonin production in plants

Melatonin is a universal amphiphilic antioxidant molecule that has strong solubility in both water and lipids and a modest size that allows it to enter all cell compartments. ROS and RNS species can be directly scavenged by melatonin, which also accelerates the function of antioxidant enzymes, protects against oxidative damage, antioxidants to produce beneficial effects, and improves electron transport capability in the mitochondrial respiratory chain to reduce electron loss and restrict the synthesis of free radicals (Roychoudhury 2023). Moreover, melatonin and its byproducts serve as naturally occurring electron donors that are highly efficient in averting oxidative stress. It can produce several radical scavengers that lead to the oxidation of molecules like β-hydroxy melatonin, cyclic β-hydroxy melatonin, and *N*1-acetyl-*N*2-formyl-5-methoxykynuramine (AFMK), as well as help to eliminate ROS (Checker et al. 2021). This property sets melatonin apart from other antioxidants and allows it to effectively shield organisms from oxidative stress, even at low concentrations. Aerobic cells' ability to efficiently perform their metabolism depends on their mitochondria, which are responsible for maintaining a proper redox status (Sachdev et al. 2021).

Melatonin has been detected in apples, barley, beans, cucumbers, grapes, lupine, maize, rice, and tomato (Salehi et al. 2019). Numerous studies conducted on 108 kinds of herbs that are commonly used in Chinese medicine have shown evidence of melatonin at concentrations ranging from thousands to a few nanograms per gram of tissue. This suggests that these herbs are great natural supplies of this important chemical for physiology (Wijesinghe et al. 2023). It has also been verified by examining melatonin's anticipated protective effect on plant photosynthesis. In general, melatonin influences the efficiency of photosynthetic processes by doing the following: slowing down the breakdown of chlorophyll, boosting the uptake of CO2, and quickening the electron transport. Beyond its ability to prevent oxidative damage, which results from both abiotic and biotic stresses, melatonin also activates several distinct plant defense mechanisms at the proteomic and genetic levels. These mechanisms protect plants from various biotic and abiotic stressors containing heavy metals, pathogens, cold, drought, heat, and light (Nawaz et al. 2023). Melatonin is a usual auxin generated from tryptophan structurally similar to indole-3-acetic acid (IAA). It has a role in the development and regulation of plant growth. Melatonin may also be involved in photoperiodic responses and the control of the circadian rhythm in plants, according to earlier studies; however, further investigation is required to completely comprehend these phenomena (Murch and Erland 2021). Studies on the chemical melatonin in plants show that it is crucial to their survival. Therefore, it is not surprising that melatonin can be found in food products and beverages made from plants, as it has been found in a large variety of edible plants and herbs (Hossain et al. 2022).

Similarities and differences between animal and plant melatonin

While the structure and functions of the chemical melatonin are similar in both plants and animals, there are distinctions in its production, regulation, and activities within each kingdom.

Similarities concerning chemical structure, biosynthetic Pathway, functions as a signaling molecule, antioxidant Properties, and regulation by Light and Circadian Rhythms. The molecular structure is conserved in both plants and animals. It is a derivative of tryptophan, an amino acid, and all living things have it in their basic structural makeup. In general, both plants and mammals share a similar melatonin biosynthesis route. Through a sequence of enzyme processes, tryptophan is converted to serotonin and subsequently to melatonin (Zhao et al. 2019). Melatonin functions as a signaling molecule in both plants and animals, helping to regulate several physiological activities. It is involved in coordinating sleep–wake cycles, circadian rhythms, and reactions to stresses in the environment. In both plants and animals, melatonin demonstrates antioxidant qualities. It contributes to cellular protection by scavenging reactive oxygen species (ROS) and reducing oxidative stress. Circadian rhythms and light are two examples of external factors that affect the generation of melatonin in plants and animals. Plants have a variety of organs that can generate melatonin in reaction to light and other environmental stimuli, but animals typically produce it in the pineal gland in response to the light–dark cycle (Tan and Reiter 2020).

Differences concerning tissues of Production, regulatory Points, physiological Roles, and localization within Cells. Animals produce melatonin in several tissues, but the pineal gland is the primary site of synthesis. Melatonin is not only produced in one organ of plants but also in a variety of tissues throughout the plant. Plants and mammals can differ in the regulatory points and enzymes involved in melatonin synthesis, even though the overall biosynthetic pathway is conserved. For instance, compared to animals, plants may have various forms and sites for *N*-acetylserotonin *O*-methyltransferase (ASMT), the enzyme in charge of the last stage of melatonin synthesis. Animals and plants can have different physiological functions for melatonin (Saha et al. 2019).

Distribution in fruit crops

Melatonin presence in various fruit crops

To meet our daily needs for the major vitamins and minerals, we frequently eat fruits and vegetables. Furthermore, fruits include several phytochemicals that control several physiological and biochemical processes, protecting against a range of chronic illnesses. After melatonin was discovered in the kingdom of plants, many researchers started looking into the amounts and purposes of this hormone in various plants. As a result, a variety of plant parts have been assessed, including seeds, roots, bulbs, and fruits. Fruits are essential foods that have also had their melatonin concentrations assessed. First noted that melatonin was present in dicotyledonous plants and described its function as a strong radical scavenger (Debnath et al. 2019). Melatonin has been found in a variety of consumable fruits. Fruits vary significantly in terms of melatonin content, even within types of the same fruit and during different phases of development as discussed in Table 2. Many techniques have been used to detect melatonin in plants, including high-performance liquid chromatography (HPLC) with electrochemical detection (HPLC-ECD), radioimmunoassay (RIA), gas chromatography-mass spectrometry (GC–MS), enzyme-linked immunosorbent assay (ELISA), and fluorescence detection (HPLC-FD). The sensitivity and specificity of each of these techniques vary (Galijašević et al. 2023).

Physiological functions of melatonin in plants

Indoleamines such as tryptophan are the precursor molecules of melatonin, and they should play a role in regulating development and growth. Because of its many physiological roles, melatonin—which is best known to assist animals in regulating their sleep and wake cycles—has become an intriguing molecule in the field of plant biology. It is produced in a variety of plant organs, such as the roots, shoots, leaves, and seeds. It works through a combination of receptor-dependent and receptor-independent pathways. Melatonin's activity as an antioxidant is one of its primary physiological roles in plants. Environmental factors like drought, salinity, high temperatures, and pollution are continual threats to plants, and they can cause oxidative stress and reactive oxygen species (ROS). Strong ROS scavenger melatonin neutralizes

Table 2 Melatonin concentration present in fruits and species

Fruits	Scientific name	Variety/cultivar	Species	Concentration (ng g^{-1})	Stage of evaluation	References
Almond	*Prunus dulcis*	–		0.12	Mature	Paroni et al. (2019)
Red grape (wine)	*Vitis vinifera* L.	Nebbiolo		0.57 to 0.63	Ripe	Fracassetti et al. (2019)
		"Nero d'Avola		0.05 to 0.62	Ripe	Fracassetti et al. (2019))
Sour cherry	*Prunus ceracus*	–		20	In the Second stage of fruit development	Tijero et al. (2019)
Goji berry/wolfberry	*Lycium barbarum*			1600.48 ± 23.66	Mature	Yılmaz (2021)
Black mulberry	*Morus nigra*			178.70 ± 0.57		
White mulberry	*Morus alba*			183.29 ± 6.27		
Blackberry	*Rubus fructicous* L.			177.91 ± 27.51		
Purple mulberry	*Morus rubra*			233.86 ± 7.20		
Bursa black mulberry	–			123.44 ± 2.05		
Cornelian cherry	*Cornus mas* L.	–	–	130.82—201.84	Mature	Uğur Y (2023)
Date Palm	*Phoenix dactylifera*	Deglet Nour	–	0.02	Mature	Verde et al. (2019)
		Allighes	–	0.0074		
		Medjbouda	–	0.02		
		Kenta	–	0.17		
		Khadrawy	–	0.0148		
		Medjou	–	0.0087		
Walnut	*Juglans regia*	Hartley	–	3.3	Mature	Verde et al. (2022a, b)
		Franquette	–	1.6		
		Pizarro	–	1.19		
		Native	–	2.07		
Apple	*Malus domestica* Mill.	Granny Smith		7.37	Ripe	Zhang et al. (2018)
		Fuji		67.63		
Mulberry	*Morus alba*	–	–	1.739 ± 0.076	Mature	Pranil et al. (2021)
Guava	*Psidium guajava*	–	–	1.570 ± 0.015	Mature	
Banana	*Musa sapientum*	–	–	1.741 ± 0.103	Ripe	
Mango	*Mangifera indica*	–	–	2.401 ± 0.036	Mature	
Pineapple	*Ananas comosus*	–	–	1.693 ± 0.088	Mature	
Orange	*Citrus sinensis*	–	–	1.704 ± 0.028	Mature	
Longan	*Dimocarpus longan*	–	–	1.676 ± 0.080	Mature	
Red passion fruit	*Passiflora edulis*	–	–	1.528 ± 0.113	Mature	
Yellow passion fruit	*Passiflora edulis*	–	–	1.744 ± 0.140	Mature	
Jujube	*Ziziphus jujuba*	–	–	1.679 ± 0.163	Mature	

ROS and shields plants from oxidative damage. Furthermore, melatonin strengthens the antioxidant defense system of plants by promoting the activity of antioxidant enzymes like catalase, peroxidases, and superoxide dismutase. Apart from its antioxidant characteristics, it controls other facets of plant growth and development. It controls flowering time, strengthens root development, and encourages seed germination and seedling growth. Additionally, it regulates stomatal mobility, which impacts plant water loss and gas exchange. It also affects how plants react to biotic stressors, such as disease invasion and herbivore assault. It has a wide range of physiological roles in plants, including growth regulation, stress responses, and antioxidant defense (Muhammad et al. 2021).

One of the most well-known properties of melatonin is its ability to scavenge free radicals triggered by oxidative stress. Furthermore, it not only controls blooming, fruit ripening, photosynthesis, senescence, apoptosis, growth cycles, root morphogenesis, seed germination, and other growth and development processes, but it also governs biotic and abiotic stress responses. As an important growth regulator for life, directly associated to plant growth and development, as well as stress responses. In plants, it can control development by influencing metabolism. It promotes kiwifruit leaf senescence by increasing the concentration of flavonoids (Zhang et al. 2021).

Antioxidant properties

The climate shift throughout the crop's growth phases makes the crops more susceptible to various abiotic stresses. Plants that are under stress produce 1–2% of the oxygen they consume into reactive oxygen species, which includes singlet oxygen (1O2), hydrogen peroxide (H_2O_2), superoxide radical (O2·−), and hydroxyl radical (·OH). Melatonin can also boost the function of antioxidant enzymes in plants. These enzymes, which include superoxide dismutase, catalase, and peroxidases, are crucial in ROS detoxification. Melatonin can promote the production and activity of these enzymes, improving the plant's antioxidant capacity. lants are continually exposed to a variety of environmental challenges, including drought, salinity, severe temperatures, and pollution, all of which can cause ROS and oxidative stress. It helps plants to deal with these challenges by scavenging ROS and maintaining cellular homeostasis. Its antioxidant function helps the plant adapt and withstand unfavorable environmental circumstances. It has been found to enhance photosynthetic efficiency in plants under stress situations (Sachdev et al. 2021). MT increases the body's natural antioxidants, like glutathione and ascorbic acid, to scavenge free radicals created under stressful conditions as discussed in Table 3. Melatonin aids in maintaining the ideal levels of photosynthetic activity, which is necessary for plant growth and productivity, by lowering oxidative damage to chloroplasts and other photosynthetic machinery. Many plant species have been shown to benefit from melatonin in terms of seed germination and seedling growth. Because of its antioxidant qualities, it may help shield seeds and young seedlings from oxidative damage during the germination and early growth stages, promoting the plant's successful establishment and growth (Hasanuzzaman et al. 2019). Melatonin administration enhanced antioxidant activity and promoted GABA production in yellow-flesh peach fruit. It drastically lowered H2O2 and MDA levels while enhancing the non-enzymatic antioxidant system (Wu et al. 2023). The application of Melatonin (100 μmol L^{-1}) applied two weeks before harvest minimized red drupelet reversion in blackberry fruit, enhancing antioxidant capacity and sustaining postharvest quality for 12 days of cold storage (Shah et al. 2023). The effect was seen with melatonin (1 μM) application with 100 mM NaCl on growth, antioxidant enzyme activity and ion hemeostasis in maize plant. The findings indicated that improvements in photosynthetic ability, antioxidant capacity, and ion homeostasis in leaves due to melatonin which enhanced salt tolerance in maize (Jiang et al. 2016).

Regulation of growth and development

Plant growth regulators (PGRs) are vital to plant development, growth, and adaptation to environmental stimuli. There are multiple widely recognized types of PGRs in plants. Salicylic and abscisic acid, ethylene, jasmonic acid, brassinosteroids, auxins, cytokinins, gibberellins, and ethylene are some of these PGRs. Auxin gradients are thought to be the most influential on deciding the consequence of morphological patterns, as they support apical dominance, cell elongation, and rooting, among other functions. On the other hand, cytokinins act as major individuals in organ development, germination, death, and the keeping up of circadian rhythms (Erland et al. 2015).

Effect of melatonin on fruit crops

Complex signaling networks control the growth and development of higher plants. Auxin, cytokinin, ethylene, and other plant hormones, together with signal molecules like calcium ions, hydrogen sulfide, and nitric oxide, work together to control essential biological processes in plants, including photosynthesis, growth, development, responses to their environment, and even senescence. At now, there is a consensus based on many lines of evidence derived from both basic and applied research that melatonin, also known as *N*-acetyl-5-methoxytryptamine, is an endogenous chemical that is highly

Table 3 Effect of different concentrations of melatonin on antioxidant and overall quality in fruits

Fruits	Best concentration	Storage temperature and days	Findings	References
Sweet cherry	100 µM	0 °C for 45 days	Retarded senescence and improved the antioxidant potential	Sharafi et al. (2021)
Sweet cherry cultivar (Prime Giant' and 'Sweet Heart)	0.3 mM	2 °C for 28 days	Enhanced antioxidant enzymes and delayed postharvest ripening process	Carrión-Antolí et al. (2022)
Blueberry	1000 µM	5 °C for 3 weeks	Increased the production of secondary metabolites and antioxidant activity	Magri et al. (2022)
	0.05 mmol L^{-1}	–	Improved the antioxidant activity and delayed the senescence	Shang et al. (2021)
Mango	1000 µmol L^{-1}	15 ± 1 °C for 4 weeks	Increased antioxidant enzymes (CAT and POD)	Rastegar et al. (2020)
Peach	0.1 mmol L^{-1}	4 °C for 28 days	Improved antioxidant activity and promoting γ-aminobutyric acid (GABA) biosynthesis	Wu et al. (2023)
Jujube	-	Room temp	Improved anti-oxidative capacity and inhibited respiratory rate	Tang et al. (2020)
'Newhall' navel orange	200 µmol L^{-1}	ambient conditions for 84 days	Enhanced antioxidant capacity and delayed postharvest senescence	Ma et al. (2021)
Strawberry Cultivars (Kabarla, Fortuna, Sweet Ann, Festival)	5 p.p.m	Open field/greenhouse	Enhanced antioxidant activity	Okatan et al. (2022)
Cape gooseberry	300 µmol L^{-1}	10 ± 1 °C for 21 days	Increased the total phenolic carotenoid and antioxidant capacity	Hayati et al. (2023)
Sweet persimmons (Youhou)	100 µM melatonin (MT) + 1 µL L^{-1} 1-methylcyclopropene (1-MCP)	0 °C for 70 days	Improving postharvest quality and antioxidant ability levels	Jiao et al. (2022)

conserved and plays a crucial role in various biological processes in plants (Qiao et al. 2019). The investigation of melatonin in plants began with the discovery of phytomelatonin, which is present in various plants and plant-derived products. Researchers have identified the essential elements of phytomelatonin production piece by piece in recent years. Compared to animal synthesis, phytomelatonin synthesis in plants is far more versatile. It has been reported that melatonin enhanced the growth of wheat seedlings in both N-sufficient and -deficient environments.

Melatonin treatment enhanced the growth parameters such as root elongation, plant height, and leaf surface area of maize seedlings (Erdal 2019).

Different developmental processes affected by melatonin

Phytomelatonin acts as a plant growth stimulator, stress protector, and flowering and fruit ripening regulator by regulating various elements related to the redox network or interfering with other phytohormones. The primary function of melatonin in plants is to serve as the first line of defense against oxidative stress, which occurs under almost all adverse environmental conditions. In cells, ROS, NO, and phytomelatonin form an interesting triad that regulates redox homeostasis, and melatonin might be the key component in the center of the redox network (Arnao and Hernández-Ruiz 2019a, 2019b). Thus, the effect of melatonin on the redox network could be used as a stimulator to develop fortified plants with, for example, anti-senescence genes and improved photosynthesis.

Abiotic stress responses

Melatonin's role in coping with environmental stressors

In terms of nutrition for humans, fruit crops are the main source of carbohydrates, minerals, micronutrients, proteins, lipids, fiber, organic acids, pigments, and antioxidants. In addition to being an essential part of a healthy diet, fruit crops help farmers in underdeveloped countries generate revenue and reduce poverty. These crops have the potential to support developing countries' economies and diversify agriculture. It is anticipated that the demand for fruits will rise significantly in the future due to a steady rise in living standards and diet. The production and yield of these crops must be increased immediately, but it is also crucial to reduce losses from abiotic stressors and pathogen infection. Drought, salinity, heat, and chilling are the main abiotic factors that can cause losses in horticultural crops of up to 50–70% as shown in Fig. 3. Typically, plants have an internal defense mechanism to lessen these pressures, but it only works up to a certain point. The natural defense mechanism is compromised by extreme stress, which results in damage and aberrant physiological conditions inside the plant cell, both of which eventually lower yields (Nowroz et al. 2024). It is anticipated that under stress conditions, melatonin biosynthesis will be upregulated, demonstrating melatonin's antistress qualities. Additionally, melatonin has a variety of physiological regulatory functions that influence plants' ability to withstand abiotic stress. Because of its detoxifying qualities, exogenously administered melatonin has a major impact on plants' capacity to withstand stress (Kaur et al. 2015).

Effect of melatonin treatment on heat stress management

Heat stress is now one of the main factors restricting fruit crop output as a result of climate change. Heat stress causes morphological, biochemical, and physiological alterations in plants that impede their ability to grow. Major enzymes are rendered inactive by high temperatures, which also restricts protein synthesis, causes photoinhibition, and accelerates the degradation of chloroplast membranes and proteins. The main negative impacts of heat stress are oxidative damage to cell proteins, lipids, and DNA, just like drought stress. Plants commonly use heat stress-induced protein in the form of self-defense (dos Santos et al. 2022).

Effect of melatonin on mitigation of salt stress

One of the most severe abiotic stresses to horticulture crops is salt stress. Salt stress has already harmed 45 million hectares (19.5% of all irrigated land) globally (Bharti and Ray 2023). Ion toxicity, osmotic stress, reactive oxygen species-mediated damage, and nutritional imbalance are among the negative impacts of salinity stress on plants. ROS overproduction is linked to membrane damage, and in salinity conditions, Na+ accumulation causes ion toxicity. In recent times, numerous studies have revealed the vital and indispensable function of melatonin in fruit crops' mitigation of salt stress, as it has been clear that the hormone is a widely distributed growth regulator

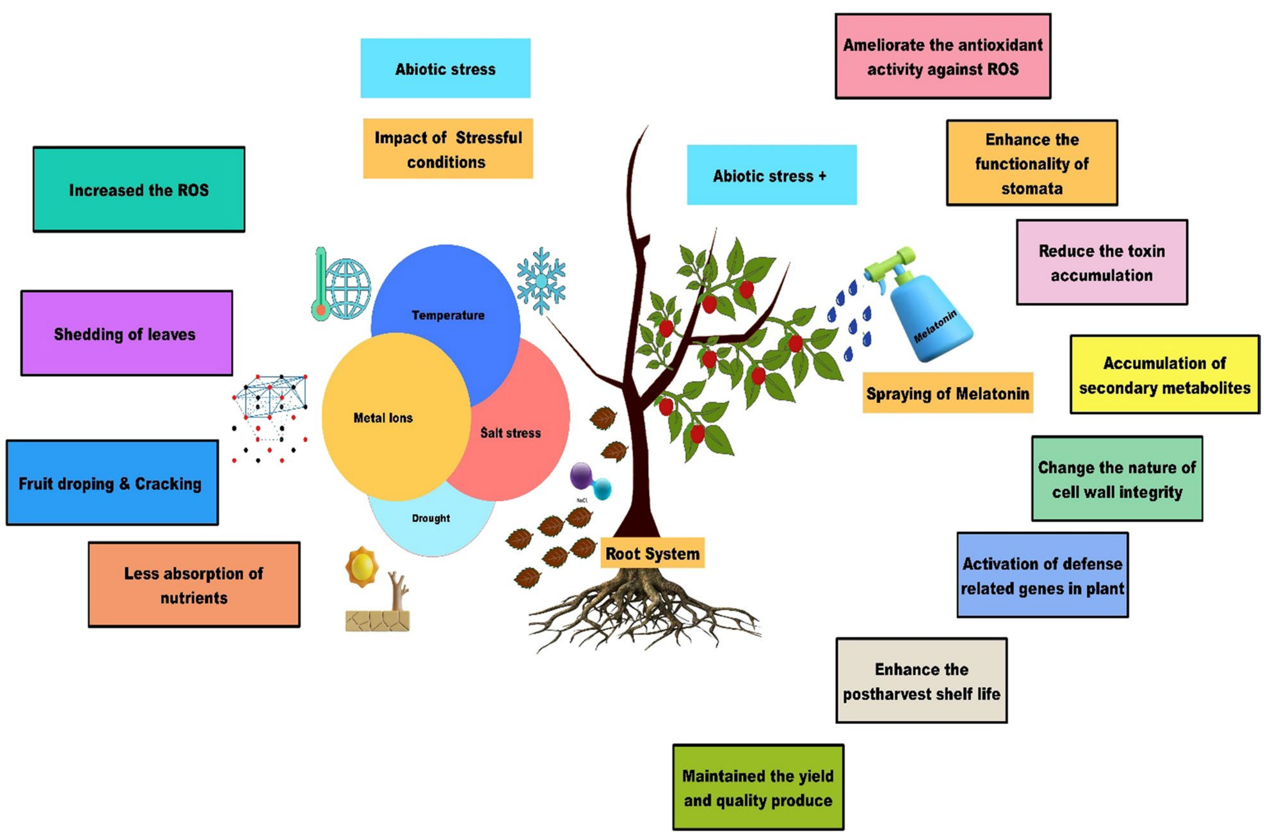

Fig. 3 Comparison between stress and Melatonin application under stressful conditions

that is essential for numerous abiotic stress resistance in plants. In salt-stressed plants, exogenous melatonin treatment may modulate both enzymatic and nonenzymatic antioxidant systems to reduce ROS-mediated damage (Gu et al. 2022). Melatonin reduced salt damage in alfalfa plants under salt stress. It significantly reduced electrolyte leakage, malondialdehyde (MDA) content, and H2O2 content, while increasing the activities of catalase (CAT), peroxidase (POD), and Cu/Zn superoxide dismutase (Cu/Zn-SOD), as well as upregulating genes related to melatonin and antioxidant enzymes biosynthesis. It functions primarily as an antioxidant, scavenging H_2O_2 and increasing the activity of antioxidant enzymes to improve alfalfa plant salt tolerance (Cen et al. 2020). Three types of grapevines were used to isolate and identify root-dwelling bacteria. It was discovered that certain bacterial strains released tryptophan-ethyl ester and melatonin when they were cultivated in a lab setting. We discovered that, in grapevine plantlets subjected to stress from salt or drought, B. amyloliquefaciens SB-9 colonization enhanced the upregulation of melatonin synthesis and its intermediates, while decreasing the upregulation of grapevine tryptophan decarboxylase genes (VvTDCs) and a serotonin *N*-acetyltransferase gene (VvSNAT) transcription (Jiao et al. 2016). Plants were able to sustain a higher photosynthetic capacity after being pretreated with 0.1 μm melatonin, which considerably reduced the growth inhibition in Malus hupehensis Rehd. under high-salinity conditions. Significant up-regulation of dNHX1 and MdAKT1 was seen in the leaves, which may have aided in maintaining ion homeostasis and enhancing salinity tolerance in plants exposed to exogenous melatonin (Li et al. 2012).

Some fruit crops have been shown to exhibit improved photosynthesis and other associated mechanisms when exposed to salt stress discussed in (Table 4).

Effect of melatonin on mitigation of cold stress

Low temperature stress can warm-climate plants and cause chilling injury which is a key abiotic problem. Both the physiological and metabolic dynamics of the cell are impacted by cold stress. The majority of the detrimental effects are similar to signs of drought stress, including damage to cell membranes, disruptions in the electron transport chain, excessive production of reactive oxygen species, unbalanced ion homeostasis, etc. Carbon fixation is hampered by cold-induced ROS buildup because it inactivates enzymes that control the Calvin cycle (Tiwari et al. 2020). Horticultural crops may exhibit morphological reactions such as uneven seed germination, reduced seedling vigor, and delayed ontogenic development, which can lead to a decrease in yield. Like other abiotic stressors, cold stress is also naturally defended against plants through enzymatic and non-enzymatic antioxidant systems, as well as increased glucose and amino acid storage to prevent osmotic damage (Zahra et al. 2021). By increasing antioxidant defense capability and modifying the DREB/CBF—COR pathway, the application

Table 4 Case studies or examples showcasing stress tolerance enhancement in fruits

Abiotic stress	Crop	Treated plant part	Plant response treated with melatonin	References
Heat stress	Kiwifruit	Seedlings	Enhanced thermal stress tolerance	Xia et al. (2021)
	Strawberry	Whole plant	Increased thermal stress tolerance	Manafi et al. (2022)
Salt stress	Strawberry	Leaves (100–200)	Increased salinity stress tolerance	Zahedi et al. (2020)
	Banana	Seedlings (100 μM)	Resistance to salt stress tolerance	Wei et al. (2022)
	Pistachio nut	Seedlings (100 μmol/L)	Increased salt stress tolerance	Kamiab (2020)
	Sour jujube	Seedlings (400 mmol/L)	Increases salt stress tolerance	Zhu et al. (2023)
Cold stress	Pomegranate	Fruit (100 μM)	Increase cold stress tolerance	Jannatizadeh (2019)
	Plum	Whole fruit	Increase cold stress tolerance	Du et al. (2023)
	Litchi	Whole fruit (0.5 mM)	Increase chilling stress tolerance	Liu et al. (2021)
	Sapota	Whole fruit (90 μM)	Reduced chilling injury	Mirshekari et al. (2020)
	Washington's navel orange	Whole fruit (1000 μM)	Reduced chilling injury	Aboryia et al. (2021)
	Guava	Whole fruit (100 μmol/ L)	Lowest chilling injury index	Chen et al. (2022)
	Mango	Whole fruit (100 μmol/L)	Reduced chilling injury development	Kebbeh et al. (2023)
Drought Stress	kiwifruit	Seedlings (100 μM)	Enhanced seedling adaptability to drought stress	Liang et al. (2019)
	Sweet cherry	Leaves (200 μM)	Increased drought tolerance	Hojjati et al. (2023)
	Citrus	Rootstocks (1.5 mM)	Increased draught tolerant	Korkmaz et al. (2022)
	Lime	Whole plant (100 μM)	Increased draught tolerant	Jafari et al. (2022)
Heavy metal stress	Apple rootstocks	Whole plant (100 μM)	Mitigated cadmium toxicity	He et al. (2020)
	Strawberry	Seedlings (100 μmol/L)	Reduced the toxic effects of Cadmium	Wu et al. (2021a, b)

of melatonin (100 μM) protects the strawberry plants against the harm caused by cold stress (Hayat et al. 2022). Melatonin treatment after harvesting kiwiberries might increase both the exterior and interior quality of the fruit and prevent senescence via altering sugar metabolism under cold storage (Zhang et al. 2023). The study examined the impact of melatonin (10 and 30 μm) on the model plant Arabidopsis thaliana, which was subjected to a cold stress at 4 °C for 72 and 120 h. The findings indicated that melatonin up-regulated genes associated with cold signaling, which could potentially promote the production of compounds that shield plants from cold stress and lead to the higher growth of plants treated with exogenous melatonin (Bajwa et al. 2014). In this work, priming-induced alterations in the maize embryo proteome were analyzed, and proteins related with priming and melatonin were identified in chilling-treated maize seeds (Kołodziejczyk et al. 2016).

Melatonin under drought stress

Plants undergo several physiological, biochemical, and molecular processes that are altered primarily by drought. Drought conditions will be harsher and last longer for plants cultivated in arid and semi-arid areas. Promoting adaptive agricultural techniques is critically needed in rapidly changing environmental conditions since various organs exhibit varying degrees of vulnerability to water stress. Enzymes involved in photosynthetic processes, including fructose-1,6-bisphosphatase (FBP) and ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco), are much less active during drought stress (Dalal 2021). These enzymes are also crucial for the Benson–Calvin cycle. Notably, excessive harmful reactive oxygen species (ROS) accumulation is the consequence of drought-induced over-reduction of the electron transport chain (ETC). Specifically, excessive accumulation of hazardous reactive oxygen species (ROS) is caused by drought-induced over-reduction of the electron transport chain (ETC). ROS may harm plants by oxidizing membrane lipids, photosynthetic pigments, proteins, and nucleic acids. Plants respond to drought stress by raising the amount of immobile nutrients through their root systems. To help with maintaining water and adapting to dry conditions, they can also change their metabolism and collect advantageous metabolites, such as proline and soluble sugar. Recent climate models predict that drought will increase in frequency throughout a large portion of the planet. Exogenous administration of plant growth regulators is one method to increase plants' resistance to drought (Farooqi et al. 2020). Pretreatment with 100 μM melatonin reduced antioxidant enzymes (POD, SOD, etc.) and osmoregulation (soluble sugars and proline) in tomato seedlings by regulating gene expression. It also improved seedling growth, root characteristics, and leaf photosynthesis under drought stress (Altaf et al. 2022). The sweet cheery trees were sprayed with melatonin at 100, 200, and 300 μM on their leaves, and their soil field capacity (FC) was measured at 75, 50, and 25%.The highest levels of AsA and phenolic contents were produced by trees exposed to drought at (50–5% FC) and treated with 200 μM of melatonin topically. Oleic acid (55.18%–68.05%) was the predominant fatty acid component, and melatonin elevated its levels while the drought lowered them (Hojjati et al. 2024). Both drought-tolerant Malus prunifolia and drought-sensitive M. hupehensis plants exhibit dramatically increased tolerance when pre-treated with melatonin. By up-regulating the expression of the melatonin synthesis genes MdTDC1, MdAANAT2, MdT5H4, and MdASMT1, plants can efficiently manage their water balance during drought circumstances.Drought-stressed plants have lower ABA concentrations because melatonin preferentially down-regulates the gene that makes ABA, MdNCED3, and up-regulates the genes that catabolize ABA, MdCYP707A1 and MdCYP707A2 (Li et al. 2015).

Melatonin under heavy metal stress

Heavy element pollutants in soil agriculture have increased as a result of the construction of factories and industries, which lowers agricultural production and economics. Heavy metal addition from diverse sources changes growth, yield, nitrogen metabolism, and photosynthesis inhibition. Melatonin helps plants grow by boosting their defense mechanisms against oxidative stress and lowering the buildup of heavy metals at the rhizospheric surface through the use of its chelating activity (Iqbal et al. 2023). Heavy metals (HMs), such as iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), molybdenum (Mo), nickel (Ni), and cobalt (Co), are necessary for plants in particular amounts, but they are harmful when are present in excess amount (Varma and Jangra 2021). Cadmium (Cd) is one of the most hazardous heavy metals for plants. Melatonin increases growth, photosynthesis, redox homeostasis, and secondary metabolites in strawberry seedlings, which may assist to mitigate phytotoxicity caused by Cadium (Saqib et al. 2023).

Biotic stress responses

Melatonin's interactions with pests and pathogens

In the horticultural system, biotic stress is commonly defined as fruit and vegetable loss resulting from infectious diseases produced by bacteria, viruses, nematodes, and insects. These biotic stressors cause plants to die and decompose in addition to directly obtaining nutrients from the plants. Pathogenic stress is a significant factor in pre- and postharvest loss of fruits. Researchers are still working to establish effective control for several viral infections that affect horticultural crops. Researchers are still trying to find efficient ways to manage various viral infections that impact horticulture crops and the surrounding environment (Umamaheswari et al. 2020). Chemical control is the most popular and successful approach because it provides quick protection and offers a wide range of management choices for its use and application. Nonetheless, there is a great need for comparatively safer compounds to manage diseases due to consumer concerns about having a food crop free of pesticides and environmental sustainability. Melatonin can serve as a biocide against certain fungi and bacteria, although there is no solid evidence on its mode of action. Melatonin has antimicrobial effect in vitro against antibiotic-resistant pathogen strains 103, whereas considerably higher concentrations have antibacterial activity against ten different human pathogenic bacteria (Arnao Hernandez-Ruiz 2015). Melatonin is an eco-friendly substance that might be used as a different tactic to help plants defend themselves against biotic stressors as shown in Fig. 4. Melatonin's preventive effect against bacterial and viral illnesses has previously been documented in animal science (Sun et al. 2021a, b). It is highly effective in both directly inhibiting the pathogen and triggering the host plant's defense response. The primary mechanisms that enable biotic stress generated by melatonin in plants are defense gene activation, cell wall thickening, and ROS scavenging. A severe threat to the worldwide horticultural production system is insect infestations. They inflict indirect costs by spreading dangerous bacterial and viral infections, as well as direct losses by eating the plants. These herbivorous insects cause the loss of one-fifth of the world's crop production annually. Melatonin is a good tool to fight insect pests, as evidenced by the growing concern about using fewer pesticides and instead relying on natural and sustainable management solutions (Giraldo Acosta et al. 2022). It is previously known that endogenous melatonin exists in the nematoda and insecta which primarily impacts circadian oscillations, photoperiodism, moulting, and seasonal rhythms (Tiwari et al. 2021a, b).

An Investigation was done to inducing resistance mechanism of melatonin treatment in a table grape. The grapes were submerged in 0.02, 0.2, and 2 mmol L^{-1} melatonin, and then 48 h later, *Botrytis cinerea* suspension injections were given. The findings indicated that exogenous melatonin treatment could stimulate defense mechanisms to fight off *B. cinerea* infection in post-harvest grapes (Li et al. 2022).

Melatonin in fruit ripening and quality

Melatonin's impact on fruit maturation

Fruit ripening is a multifaceted process controlled by hormones and genes that involves several metabolic, physiological, and structural alterations (Table 5). When it comes to hormones, ethylene is crucial in regulating a variety of the mechanisms involved in fruit ripening. In climacteric fruits, the release of ethylene and respiration rate rise during fruit ripening (Li et al. 2021). A typical climacteric fruit takes around four weeks to ripen, and ethylene is a key regulator of the flavor, aroma, color, and softening changes that occur during this time and ultimately determine the fruit's final quality. Other chemicals that have regulatory roles in fruit ripening are also integrated, such as auxin, salicylic acid, jasmonic acid, and abscisic acid. Physiological nitro-oxidative stress associated with fruit ripening has been discovered recently. This stress affects numerous subcellular processes, causing some metabolic pathways to be up and down-regulated. These effects include delaying fruit senescence, reducing chilling injury, reducing fungal decay, and enhancing nutritional quality (Fenn and Giovannoni 2021). The study examined the growth and ripening as well as the impact of melatonin (500 μM) on the apple tree. Melatonin treatment dramatically enhanced ethylene production while also increasing fruit size, weight, sugar content, and firmness. Melatonin appears to enhance fruit ripening by inducing ethylene production, whereas melatonin treatments prior to ripening increase ultimate fruit quality (Verde et al. 2020a, b).

Implications for fruit quality and post-harvest characteristics

Fruit's delicious flavor and abundance of nutrients (such as vitamins, organic acids, and polyphenolic compounds) have made it a popular meal choice for people all over the world. Fruits are perishable and need quick postharvest storage, which diminishes their taste and nutritional value and negatively impacts consumer acceptance as well as the financial value of fresh produce (Palumbo et al. 2022). Thus, scientists have always been concerned with how to preserve the quality of postharvest fruit throughout storage. In contrast to fruit ripening, senescence is characterized by a progressive decline in fruit quality. Fruit senescence is a phase in which the tissue structure and nutritional components gradually deteriorate as the ability to maintain the internal environment and adapt to the storage environment gradually declines. The senescence of postharvest during storage has been proven to be considerably delayed by exogenous melatonin therapy, extending the shelf life (Zhang et al. 2019a, b). Fruit firmness was preserved by melatonin treatment, which also decreased weight loss, respiration rate, and weight loss while maintaining levels of TSS and soluble sugar and preventing browning of the peel and flesh (Chen et al. 2022). The study examined melatonin affected the postharvest quality of nectarine fruit (cv. Fantasia). Fruits were stored for 40 days at 0–1 °C and 85–90% relative humidity after being immersed in melatonin concentrations (control, 250, 500, and 1000 µmol L^{-1}). It prolonged the postharvest life of nectarine fruits, keeping their appearance and nutritional content, and decreasing the loss of health-promoting compounds (Bal 2021). An investigation was done on exogenous melatonin treatment which greatly inhibited postharvest physiological deterioration (PPD) of cassava tuberous roots by lowering H2O2 levels and enhancing catalase and peroxidase activity. Taken together, this study gives new insights into melatonin's influence and underlying process on PPD delay, as well as a viable technique for prolonging shelf life and improving cassava tuberous roots (Hu et al. 2016).

Research gaps, challenges future prospects, and implications

A naturally occurring substance in food is melatonin. Research has indicated that melatonin is available in various fruit types and that the precise amount is determined by several variables, such as the type of fruit and

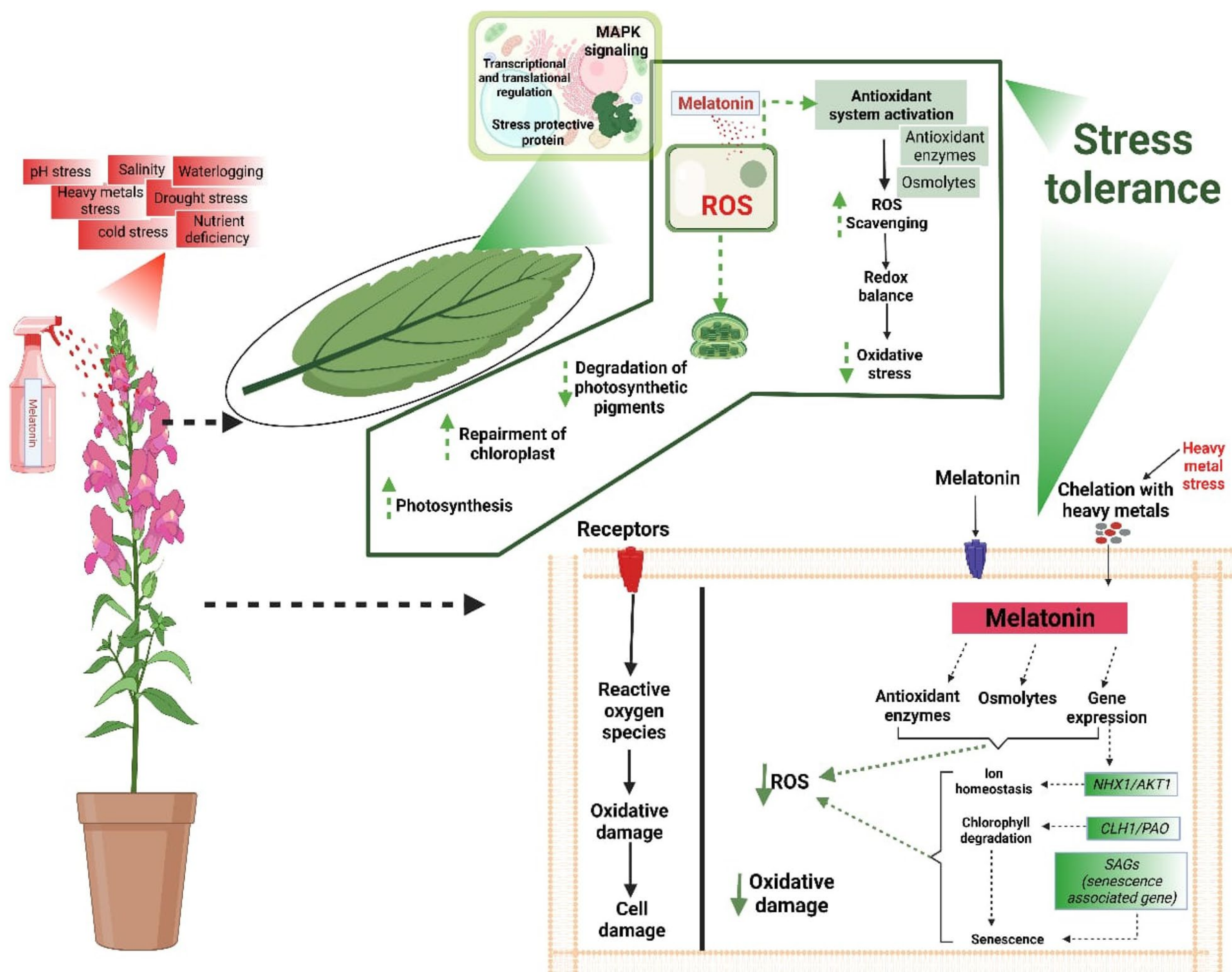

Fig. 4 Melatonin application and their entry into cellular membranes and immediately eliminates reactive oxygen species (ros) and ameliorate the osmolytes, safeguards the photosynthetic apparatus, preserves the redox balance, and influences the signalling transduction and gene expression associated with various stresses to promote stress tolerance. Adopted from (Hassan et al. 2022) under the terms of the Creative Commons Attribution License (CC BY)

its level of ripeness, genetic characteristics, growing circumstances, environmental stressors, and laboratory technique. Though the controlled processes of melatonin based on fruit ripening remain incompletely understood, recent studies have focused more on studying the links between melatonin content and the fruit ripening stage. Surprisingly, there hasn't been any research done on how postharvest modifications that extend fruit shelf life affect melatonin levels. The comprehension of melatonin's physiological functions during ripening could be enhanced by this information. The most difficult aspect of the research on melatonin in fruits is still obtaining established analytical methodologies with sufficient sample preparation to reliably estimate the amount of melatonin in fruits. More precise analytical techniques are required to get consistent results in fruits so that data on the effects of dietary melatonin may be gathered. Even though a recent study confirmed that SNAT is present in plants for the first time and that ASMT is the enzyme that limits the pace at which melatonin is biosynthesized, more research needs to be done on the melatonin synthesized pathway in fruits. It's uncertain if the proposed plant biosynthetic pathway is widespread or not. According to studies, melatonin in fruits primarily acts as the primary protection against oxidative stressors, which are put on by toxins from internal and from the environment. It is still unclear whether melatonin's potential to act as an antioxidant in fruits depends just on its direct interaction with ROS or if melatonin receptors also play a role. There is no evidence of melatonin receptors in fruits. In addition to its role as an antioxidant, melatonin has the potential to enhance plants' ability to remove various contaminants, including heavy metals, through phytoremediation. Finally, because fruit has biological functions, it may affect the endogenous melatonin level and thereby improve human health.

Melatonin has been shown in recent research to have a wide range of potential applications in horticultural fields, such as food safety, virus-free plant development, vegetative reproduction, molecular breeding, and crop processing. Important plant functions like parthenocarpy, autophagy, and arbuscular mycorrhizal symbiosis can all be impacted by melatonin. Fruit growth and defense have been linked to endogenous melatonin, whose concentrations change as the fruit ripens, peaking before veraison and falling over the rest of the fruit's development. Research has shown that applying this treatment to plants increases fruit weight and quantity, which in turn increases crop yield. Direct application reduced oxidative stress in fruit and encouraged the suppression of fruit senescence. The fruit that has been treated has a higher ratio of unsaturated to saturated fatty

Table 5 Potential applications of melatonin to overcome pest and disease management in fruit crops

Fruits	Pathogen/Disease	Treated part with concentration	Impact on fruit	References
Grape	*Botrytis cinerea*	Berries (2 mmol/L^{-1})	Inhibited an increase in cell membrane permeability and activated defence responses	Li et al. (2022)
Apple	Anthracnose	600 µmol/L	Enhanced resistance to anthracnose disease	Fan et al. (2022a, b)
Jujube	Alternaria rot	200 µmol/L	prolonged the disease resistance by managing reactive oxygen species metabolism	Zhang et al. (2022a, b)
Papaya	Anthracnose	400 µmol/L	delayed fruit softening and reducing anthracnose incidence	Fan et al. (2022a, b)
Citrus	Green mold (*Penicillium digitatum*)	–	Decreased resistance to green mold	Lin et al. (2019)
Blueberry	*Alternaria alternata, Botrytis cinerea, and Colletotrichum gloeosporioides*	0.3 mmol/L	Induced the activation of jasmonic acid signaling and phenylpropane pathways as defense responses	Qu et al. (2022)
Strawberry	Gray mold (*Botrytis cinerea*)	100 µM	Enhanced the gathering of DPPH scavenging capacity and reduced *B. cinerea* infection	Promyou et al. (2023)
Litchi	Downy blight	–	induced resistance to downy blight by modulating the phenylpropanoid and pentose phosphate pathways	Zhang et al. (2021)
Pear	*Botryosphaeria dothidea*	100 µM	Increased resistance to *B. dothidea* by enhancing the autophagic activity and soluble sugar/organic acid accretion	Wang et al. (2022a, b)
Apple	Gray mold	(*Meyerozyma guilliermondii* Y-1 (1 × 10-8 cells/mL+ 100 µmol/L)	Effective against gray mold	Sun et al. (2021a, b)

acids, which has been shown to enhance its resistance to chilling stress. In-vitro fruit pathogen-fighting properties of melatonin have been demonstrated against oomycete and fungal infections (Wang et al. 2020a).

Conclusion and way forward

The evolution of new varieties and the application of melatonin as an innovative, environmentally friendly agrochemical have an enormous ability to address agricultural difficulties by controlling plant growth, prolonging the conservation of postharvest crops, and boosting resilience to biotic and abiotic stresses.. Some climacteric fruits, like mangos, bananas, kiwifruits, avocados, and bananas, must be harvested before the climacteric phase to prolong their shelf life. These fruits can also be artificially ripened with ethephon. Melatonin is anticipated to be utilized, similar to other PGRs, to enhance the agronomic qualities of horticulture plants. In addition to its health benefits, melatonin can enhance the body's natural production of other advantageous compounds including phenols and anthocyanins. Additionally possessing significant antioxidant qualities, phenolic substances may offer protection against neurological and cardiovascular illnesses. Finally, several horticultural crop examples have indicated the creation of novel crop cultivars, and the application of melatonin as a PGR, antibacterial, and preservative has a significant ability to tackle major issues faced by the horticulture sector. A naturally occurring substance called melatonin helps plants withstand environmental stresses including salinity, drought, and high temperatures, which improves fruit quality and yield. Because of its antioxidant qualities, plants may respond to stress better and adjust to shifting climates more successfully. Furthermore, supplementing with melatonin can improve growth conditions, lessen the need for artificial agrochemicals, and encourage environmentally friendly farming methods. In light of these issues, melatonin integration into agricultural practices provides a sustainable alternative to increase fruit yield, guaranteeing environmental preservation and food security. Therefore, field experiments should be used to evaluate any possible uses for melatonin. It is also necessary to obtain melatonin from less costly sources.

Acknowledgements

The authors are grateful to the Department of Fruit Science of Lovely Professional University and Dr YS Parmar University of Horticulture and Forestry, Nauni for the valuable support.

Author contributions

Hi, SS, VSR: (writing—original draft preparation); Hi, SS, VT, An, Pr, AK, and ST (Figures and Tables); Hi, VSR and SS (conceptualization and supervision); SS and Hi (helped in data compilation and arrangement); SS, Hi, VSR NS and ST (reviewed the write-up and helped in finalizing the draft).

Funding

No funding is available.

Data availability

Not applicable.

Declarations

Competing interests

No conflict of interest.

Received: 23 April 2024 Accepted: 24 October 2024

Published online: 04 November 2024

References

Aboryia MS, Lo'ay AA, Omar AS. Reduction of chilling injury of 'Washington'navel orange fruits by melatonin treatments during cold storage. Folia Horticult. 2021;33(2):343–53.

Agathokleous E, Kitao M, Calabrese EJ. New insights into the role of melatonin in plants and animals. Chem Biol Interact. 2019;299:163–7.

Altaf MA, Shahid R, Ren MX, Naz S, Altaf MM, Khan LU, et al. Melatonin improves drought stress tolerance of tomato by modulating plant growth, root architecture, photosynthesis, and antioxidant defense system. Antioxidants. 2022;11(2):309.

Arnao MB, Hernández-Ruiz J. Functions of melatonin in plants: a review. J Pineal Res. 2015;59(2):133–50.

Arnao MB, Hernández-Ruiz J. Melatonin: a new plant hormone and/or a plant master regulator? Trends Plant Sci. 2019a;24:38–48.

Arnao MB, Hernández-Ruiz J. Melatonin and reactive oxygen and nitrogen species: a model for the plant redox network. Melatonin Res. 2019b;2:152–68.

Arnao MB, Hernández-Ruiz J. Melatonin in flowering, fruit set, and fruit ripening. Plant Reprod. 2020;33:77–87.

Ayyaz A, Shahzadi AK, Fatima S, Yasin G, Zafar ZU, Athar HUR, Farooq MA. Uncovering the role of melatonin in plant stress tolerance. Theor Exp Plant Physiol. 2022;34(3):335–46.

Bajwa VS, Shukla MR, Sherif SM, Murch SJ, Saxena PK. Role of melatonin in alleviating cold stress in *Arabidopsis thaliana*. J Pineal Res. 2014;56(3):238–45.

Bal E. Effect of melatonin treatments on biochemical quality and postharvest life of nectarines. J Food Meas Charact. 2021;15(1):288–95.

Bharti P, Ray PK. Management of salt affected soils for ensuring food security. Agriculture & food e-newsletter; 2023.

Bulgari R, Franzoni G, Ferrante A. Biostimulants application in horticultural crops under abiotic stress conditions. Agronomy. 2019;9(6):306.

Cao S, Shao J, Shi L, Xu L, Shen Z, Chen W, Yang Z. Melatonin increases chilling tolerance in postharvest peach fruit by alleviating oxidative damage. Sci Rep. 2018;8(1):806.

Cao Y, Zhang J, Du P, Ji J, Zhang X, Xu J, et al. Melatonin alleviates cadmium toxicity by regulating root endophytic bacteria community structure and metabolite composition in apples. Tree Physiol. 2024;44:009.

Carrión-Antolí A, Lorente-Mento JM, Valverde JM, Castillo S, Valero D, Serrano M. Effects of melatonin treatment on sweet cherry tree yield and fruit quality. Agronomy. 2021;12(1):3.

Carrión-Antolí A, Martínez-Romero D, Guillén F, Zapata PJ, Serrano M, Valero D. Melatonin pre-harvest treatments leads to maintenance of sweet cherry quality during storage by increasing antioxidant systems. Front Plant Sci. 2022;13: 863467.

Cen H, Wang T, Liu H, Tian D, Zhang Y. Melatonin application improves salt tolerance of alfalfa (*Medicago sativa* L.) by enhancing antioxidant capacity. Plants. 2020;9(2):220.

Checker R, Patwardhan RS, Jayakumar S, Maurya DK, Bandekar M, Sharma D, Sandur SK. Chemical and biological basis for development of novel radioprotective drugs for cancer therapy. Free Radical Res. 2021;55(8):828–58.

Chen H, Lin H, Jiang X, Lin M, Fan Z. Amelioration of chilling injury and enhancement of quality maintenance in cold-stored guava fruit by melatonin treatment. Food Chem X. 2022;14: 100297.
Cramer C, Chisoro-Dube S. The industrialization of freshness and structural transformation in South African fruit exports. In: structural transformation in South Africa. Oxford University Press; 2021. p. 120–42.
Dai L, Li J, Harmens H, Zheng X, Zhang C. Melatonin enhances drought resistance by regulating leaf stomatal behaviour, root growth and catalase activity in two contrasting rapeseed (*Brassica napus* L.) genotypes. Plant Physiol Biochem. 2020;149:86–95.
Dalal VK. Modulation of photosynthesis and other proteins during water–stress. Mol Biol Rep. 2021;48(4):3681–93.
Debnath B, Islam W, Li M, Sun Y, Lu X, Mitra S, et al. Melatonin mediates enhancement of stress tolerance in plants. Int J Mol Sci. 2019;20(5):1040.
dos Santos TB, Ribas AF, de Souza SGH, Budzinski IGF, Domingues DS. Physiological responses to drought, salinity, and heat stress in plants: a review. Stresses. 2022;2(1):113–35.
Du H, Liu D, Liu G, Liu H, Kurtenbach R. Polyamines conjugated to the bio-membranes and membrane conformations are involved in the melatonin-mediated resistance of harvested plum fruit to cold stress. Postharvest Biol Technol. 2023;204: 112480.
El-Naby A, Abdelkhalek Ahmed Mohamed M, El-Naggar YIM. Effect of melatonin, GA3 and NAA on vegetative growth, yield and quality of 'Canino'apricot fruits. Acta Scientiarum Polonorum. Hortorum Cultus. 2019;18(3):167–74.
Erdal S. Melatonin promotes plant growth by maintaining integration and coordination between carbon and nitrogen metabolisms. Plant Cell Rep. 2019;38:1001–12.
Erland LA, Murch SJ, Reiter RJ, Saxena PK. A new balancing act: the many roles of melatonin and serotonin in plant growth and development. Plant Signal Behav. 2015;10(11): e1096469.
Erland LA, Saxena PK, Murch SJ. Melatonin in plant signalling and behaviour. Funct Plant Biol. 2017;45(2):58–69.
Fan S, Li Q, Feng S, Lei Q, Abbas F, Yao Y, et al. Melatonin maintains fruit quality and reduces anthracnose in postharvest papaya via enhancement of antioxidants and inhibition of pathogen development. Antioxidants. 2022a;11(5):804.
Fan S, Xiong T, Lei Q, Tan Q, Cai J, Song Z, et al. Melatonin treatment improves postharvest preservation and resistance of guava fruit (*Psidium guajava* L.). Foods. 2022b;11(3):262.
Farooqi ZUR, Ayub MA, Ur Rehman MZ, Sohail MI, Usman M, Khalid H, Naz K. Regulation of drought stress in plants. In: Plant life under changing environment. Academic Press; 2020. p. 77–104.
Fenn MA, Giovannoni JJ. Phytohormones in fruit development and maturation. Plant J. 2021;105(2):446–58.
Fracassetti D, Vigentini I, Lo Faro AFF, De Nisi P, Foschino R, Tirelli A, et al. Assessment of tryptophan, tryptophan ethylester, and melatonin derivatives in red wine by SPE-HPLC-FL and SPE-HPLC-MS methods. Foods. 2019;8(3):99.
Galijašević S, Burović S, Stambolić A, Omanović-Mikličanin E. Phytomelatonin: recent advances-systematic. In: 32nd scientific-expert conference of agriculture and food industry: local food production systems in the era of global challenges. Springer Nature; 2023. p. 387.
Gamage A, Gangahagedara R, Gamage J, Jayasinghe N, Kodikara N, Suraweera P, Merah O. Role of organic farming for achieving sustainability in agriculture. Farm Syst. 2023;1(1): 100005.
Gao Y, Chen H, Chen D, Hao G. Genetic and evolutionary dissection of melatonin response signaling facilitates the regulation of plant growth and stress responses. J Pineal Res. 2023;74(2): e12850.
Giraldo Acosta M, Cano A, Hernández-Ruiz J, Arnao MB. Melatonin as a possible natural safener in crops. Plants. 2022;11(7):890.
Gökbayrak Z, Engin H, Kiraz H. Effects of melatonin and IAA on adventitious root formation in rootstock 5BB and cv. cabernet sauvignon (*Vitis vinifera* L.). Kahramanmaraş Sütçü İmam Üniversitesi Tarım Ve Doğa Dergisi. 2020;23(4):835–41.
Golovin A, Derkach N, Zyukin D. Development of food exports to ensure economic security. Econ Annals-XX. 2020;I:186.
Gu Q, Xiao Q, Chen Z, Han Y. Crosstalk between melatonin and reactive oxygen species in plant abiotic stress responses: an update. Int J Mol Sci. 2022;23(10):5666.
Gyawali P, Bhandari S, Shrestha J. Horti-tourism; an approach for strengthening farmers' economy in the post-covid situation. J Agric Food Res. 2022;7: 100278.
Hasanuzzaman M, Bhuyan MB, Anee TI, Parvin K, Nahar K, Mahmud JA, Fujita M. Regulation of ascorbate-glutathione pathway in mitigating oxidative damage in plants under abiotic stress. Antioxidants. 2019;8(9):384.
Hassan M U, Mahmood A., Awan M I, Maqbool R, Aamer M, Alhaithloul H A, Qari S H. Melaton–ininduced protection against plant abiotic stress: mechanisms and prospects. Frontiers in plant science. 2022;13:902694.
Hayat F, Sun Z, Ni Z, Iqbal S, Xu W, Gao Z, et al. Exogenous melatonin improves cold tolerance of strawberry (*Fragaria*× *ananassa* Duch.) through modulation of DREB/CBF-COR pathway and antioxidant defense system. Horticulturae. 2022;8(3):194.
Hayati P, Hosseinifarahi M, Abdi G, Radi M, Taghipour L. Melatonin treatment improves nutritional value and antioxidant enzyme activity of *Physalis peruviana* fruit during storage. J Food Meas Charact. 2023;17:1–10.
He J, Zhuang X, Zhou J, Sun L, Wan H, Li H, Lyu D. Exogenous melatonin alleviates cadmium uptake and toxicity in apple rootstocks. Tree Physiol. 2020;40(6):746–61.
Hojjati M, Jahromi MG, Abdossi V, Torkashvand AM. Exogenous melatonin modulated drought stress by regulating physio-biochemical attributes and fatty acid profile of sweet cherry (*Prunus avium* L.). J Plant Growth Regul. 2024;43(1):299–313.
Hossain A, Pamanick B, Venugopalan VK, Ibrahimova U, Rahman MA, Siyal AL, et al. Emerging roles of plant growth regulators for plants adaptation to abiotic stress–induced oxidative stress. In: Emerging plant growth regulators in agriculture. Academic Press; 2022. p. 1–72.
Hu W, Kong H, Guo Y, Zhang Y, Ding Z, Tie W, et al. Comparative physiological and transcriptomic analyses reveal the actions of melatonin in the delay of postharvest physiological deterioration of cassava. Front Plant Sci. 2016;7:736.
Hu W, Yang H, Tie W, Yan Y, Ding Z, Liu Y, et al. Natural variation in banana varieties highlights the role of melatonin in postharvest ripening and quality. J Agric Food Chem. 2017;65(46):9987–94.
Hussain A, Faizan M, Ahmed SM. Regulation of photosynthesis by melatonin under optimal and suboptimal conditions. In: Melatonin in plants: role in plant growth, development, and stress response. Springer Nature Singapore: Singapore; 2024. p. 35–51.
Iqbal N, Tanzeem-ul-Haq HS, Turan V, Iqbal M. Soil amendments and foliar melatonin reduced Pb uptake, and oxidative stress, and improved spinach quality in Pb-contaminated soil. Plants. 2023;12(9):1829.
Ivanov D, Mazzoccoli G, Anderson G, Linkova N, Dyatlova A, Mironova E, et al. Melatonin, its beneficial effects on embryogenesis from mitigating oxidative stress to regulating gene expression. Int J Mol Sci. 2021;22(11):5885.
Jafari M, Shahsavar AR, Talebi M, Hesami M. Exogenous melatonin protects lime plants from drought stress-induced damage by maintaining cell membrane structure, detoxifying ROS and regulating antioxidant systems. Horticulturae. 2022;8(3):257.
Jannatizadeh A. Exogenous melatonin applying confers chilling tolerance in pomegranate fruit during cold storage. Sci Hortic. 2019;246:544–9.
Jiang C, Cui Q, Feng K, Xu D, Li C, Zheng Q. Melatonin improves antioxidant capacity and ion homeostasis and enhances salt tolerance in maize seedlings. Acta Physiol Plant. 2016;38:1–9.
Jiao J, Ma Y, Chen S, Liu C, Song Y, Qin Y, et al. Melatonin-producing endophytic bacteria from grapevine roots promote the abiotic stress-induced production of endogenous melatonin in their hosts. Front Plant Sci. 2016;7:1387.
Jiao X, Deng B, Zhang L, Gao Z, Feng Z, Wang R. Melatonin and 1-methylcyclopropene improve the postharvest quality and antioxidant capacity of 'Youhou'sweet persimmons during cold storage. Int J Fruit Sci. 2022;22(1):809–25.
Juhnevica-Radenkova K, Moreno DA, Ikase L, Drudze I, Radenkovs V. Naturally occurring melatonin: Sources and possible ways of its biosynthesis. Comp Rev Food Sci Food Saf. 2020;19(6):4008–30.
Kamiab F. Exogenous melatonin mitigates the salinity damages and improves the growth of pistachio under salinity stress. J Plant Nutr. 2020;43(10):1468–84.

Kaur H, Mukherjee S, Baluska F, Bhatla SC. Regulatory roles of serotonin and melatonin in abiotic stress tolerance in plants. Plant Signal Behav. 2015;10(11): e1049788.

Kaya C, Ugurlar F. Melatonin and stress tolerance in horticultural crops: Insights into gene regulation, epigenetic modifications, and hormonal interplay. Sci Hortic. 2023;322: 112432.

Kebbeh M, Dong JX, Chen HUAN, Yan LIU, Zheng XL. Melatonin treatment alleviates chilling injury in mango fruit 'Keitt'by modulating proline metabolism under chilling stress. J Integr Agric. 2023;22(3):935–44.

Khalil HB, Kamel AM, Mohamed AY, Hesham D, Mahmoud Y, Ibrahim R, et al. Emerging roles of melatonin in mitigating pathogen stress. In: Melatonin: role in plant signaling, growth and stress tolerance: phytomelatonin in normal and challenging environments. Cham: Springer International Publishing; 2023. p. 237–48.

Khan A, Numan M, Khan AL, Lee IJ, Imran M, Asaf S, Al-Harrasi A. Melatonin: awakening the defense mechanisms during plant oxidative stress. Plants. 2020;9(4):407.

Kołodziejczyk I, Dzitko K, Szewczyk R, Posmyk MM. Exogenous melatonin improves corn (*Zea mays* L.) embryo proteome in seeds subjected to chilling stress. J Plant Physiol. 2016;193:47–56.

Korkmaz N, Aşkin MA, Altunlu H, Polat M, Okatan V, Kahramanoğlu İ. The effects of melatonin application on the drought stress of different citrus rootstocks. Turk J Agric for. 2022;46(4):585–600.

Li C, Wang P, Wei Z, Liang D, Liu C, Yin L, et al. The mitigation effects of exogenous melatonin on salinity-induced stress in *Malus hupehensis*. J Pineal Res. 2012;53(3):298–306.

Li C, Tan DX, Liang D, Chang C, Jia D, Ma F. Melatonin mediates the regulation of ABA metabolism, free-radical scavenging, and stomatal behaviour in two *Malus* species under drought stress. J Exp Bot. 2015;66(3):669–80.

Li S, Chen K, Grierson D. Molecular and hormonal mechanisms regulating fleshy fruit ripening. Cells. 2021;10(5):1136.

Li Z, Zhang S, Xue J, Mu B, Song H, Liu Y. Exogenous melatonin treatment induces disease resistance against *Botrytis cinerea* on post-harvest grapes by activating defence responses. Foods. 2022;11(15):2231.

Liang D, Ni Z, Xia H, Xie Y, Lv X, Wang J, et al. Exogenous melatonin promotes biomass accumulation and photosynthesis of kiwifruit seedlings under drought stress. Sci Hortic. 2019;246:34–43.

Lin Y, Fan L, Xia X, Wang Z, Yin Y, Cheng Y, Li Z. Melatonin decreases resistance to postharvest green mold on citrus fruit by scavenging defense-related reactive oxygen species. Postharvest Biol Technol. 2019;153:21–30.

Liu S, Huang H, Huber DJ, Pan Y, Shi X, Zhang Z. Delay of ripening and softening in 'Guifei'mango fruit by postharvest application of melatonin. Postharvest Biol Technol. 2020;163: 111136.

Liu J, Sun J, Pan Y, Yun Z, Zhang Z, Jiang G, Jiang Y. Endogenous melatonin generation plays a positive role in chilling tolerance in relation to redox homeostasis in litchi fruit during refrigeration. Postharvest Biol Technol. 2021;178: 111554.

Liu G, Hu Q, Zhang X, Jiang J, Zhang Y, Zhang Z. Melatonin biosynthesis and signal transduction in plants in response to environmental conditions. J Exp Bot. 2022;73(17):5818–27.

Ma Q, Lin X, Wei Q, Yang X, Zhang YN, Chen J. Melatonin treatment delays postharvest senescence and maintains the organoleptic quality of 'Newhall'navel orange (*Citrus sinensis* (L.) Osbeck) by inhibiting respiration and enhancing antioxidant capacity. Scientia Horticult. 2021;286: 110236.

Magri A, Petriccione M. Melatonin treatment reduces qualitative decay and improves antioxidant system in highbush blueberry fruit during cold storage. J Sci Food Agric. 2022;102(10):4229–37.

Manafi H, Baninasab B, Gholami M, Talebi M, Khanizadeh S. Exogenous melatonin alleviates heat-induced oxidative damage in strawberry (*Fragaria*× *ananassa* Duch. Cv. Ventana) Plant. J Plant Growth Regul. 2022;41:1–13.

Mannino G, Pernici C, Serio G, Gentile C, Bertea CM. Melatonin and phytomelatonin: chemistry, biosynthesis, metabolism, distribution and bioactivity in plants and animals—an overview. Int J Mol Sci. 2021;22(18):9996.

Mao J, Niu C, Li K, Chen S, Tahir MM, Han M, Zhang D. Melatonin promotes adventitious root formation in apple by promoting the function of MdWOX11. BMC Plant Biol. 2020;20(1):1–11.

Medina-Santamarina J, Serrano M, Lorente-Mento JM, García-Pastor ME, Zapata PJ, Valero D, Guillén F. Melatonin treatment of pomegranate trees increases crop yield and quality parameters at harvest and during storage. Agronomy. 2021;11(5):861.

Mir AR, Faizan M, Bajguz A, Sami F, Siddiqui H, Hayat S. Occurrence and biosynthesis of melatonin and its exogenous effect on plants. Acta Soc Bot Pol. 2020. https://doi.org/10.5586/asbp.8922.

Mirshekari A, Madani B, Yahia EM, Golding JB, Vand SH. Postharvest melatonin treatment reduces chilling injury in sapota fruit. J Sci Food Agric. 2020;100(5):1897–903.

Muhammad I, Shalmani A, Ali M, Yang QH, Ahmad H, Li FB. Mechanisms regulating the dynamics of photosynthesis under abiotic stresses. Front Plant Sci. 2021;11: 615942.

Murch SJ, Erland LA. A systematic review of melatonin in plants: an example of evolution of literature. Front Plant Sci. 2021;12: 683047.

Nawaz M, Sun J, Shabbir S, Khattak WA, Ren G, Nie X, et al. A review of plants strategies to resist biotic and abiotic environmental stressors. Sci Total Environ. 2023;900: 165832.

Nowroz F, Hasanuzzaman M, Siddika A, Parvin K, Caparros PG, Nahar K, Prasad PV. Elevated tropospheric ozone and crop production: potential negative effects and plant defense mechanisms. Front Plant Sci. 2024;14:1244515.

Okatan V, Aşkın MA, Polat M, Bulduk I, Çolak AM, Güçlü SF, et al. Effects of melatonin dose on fruit yield, quality, and antioxidants of strawberry cultivars grown in different crop systems. Agriculture. 2022;13(1):71.

Omotayo AO, Aremu AO. Underutilized African indigenous fruit trees and food–nutrition security: opportunities, challenges, and prospects. Food Energy Secur. 2020;9(3): e220.

Palumbo M, Attolico G, Capozzi V, Cozzolino R, Corvino A, de Chiara MLV, et al. Emerging postharvest technologies to enhance the shelf-life of fruit and vegetables: an overview. Foods. 2022;11(23):3925.

Pan, Y, Xu X, Li L, Sun Q, Wang Q, Huang H, Zhang J. Melatonin-mediated development and abiotic stress tolerance in plants. Frontiers in Plant Science. 2023;14:1100827.

Paroni R, Dei Cas M, Rizzo J, Ghidoni R, Montagna MT, Rubino FM, Iriti M. Bioactive phytochemicals of tree nuts. Determination of the melatonin and sphingolipid content in almonds and pistachios. J Food Compos Anal. 2019;82: 103227.

Pranil T, Moongngarm A, Manwiwattanakul G, Loypimai P, Kerr WL. Melatonin and its derivative contents in tropical fruits and fruit tablets. J Food Compos Anal. 2021;103: 104109.

Promyou S, Raruang Y, Chen ZY. Melatonin treatment of strawberry fruit during storage extends its post-harvest quality and reduces infection caused by *Botrytis cinerea*. Foods. 2023;12(7):1445.

Qiao Y, Yin L, Wang B, Ke Q, Deng X, Wang S. Melatonin promotes plant growth by increasing nitrogen uptake and assimilation under nitrogen deficient condition in winter wheat. Plant Physiol Biochem. 2019;139:342–9.

Qu G, Wu W, Ba L, Ma C, Ji N, Cao S. Melatonin enhances the postharvest disease resistance of blueberries fruit by modulating the jasmonic acid signaling pathway and phenylpropanoid metabolites. Front Chem. 2022;10: 957581.

Ramasamy K, Karuppasami KM, Alagarswamy S, Shanmugam KP, Rathinavelu S, Vellingiri G, et al. Role of melatonin in directing plant physiology. Agronomy. 2023;13(9):2405.

Rastegar S, Khankahdani HH, Rahimzadeh M. Effects of melatonin treatment on the biochemical changes and antioxidant enzyme activity of mango fruit during storage. Scientia Horticult. 2020;259: 108835.

Roychoudhury A, editor. Advancement of melatonin research in plants: multifaceted role in regulating development and stress protection. CRC Press; 2023.

Sachdev S, Ansari SA, Ansari MI, Fujita M, Hasanuzzaman M. Abiotic stress and reactive oxygen species: generation, signaling, and defense mechanisms. Antioxidants. 2021;10(2):277.

Saha S, Singh KM, Gupta BBP. Melatonin synthesis and clock gene regulation in the pineal organ of teleost fish compared to mammals: similarities and differences. Gen Comp Endocrinol. 2019;279:27–34.

Salehi B, Sharopov F, Fokou PVT, Kobylinska A, Jonge LD, Tadio K, et al. Melatonin in medicinal and food plants: occurrence, bioavailability, and health potential for humans. Cells. 2019;8(7):681.

Saqib M, Shahzad U, Zulfiqar F, Tiwari RK, Lal MK, Naz S, et al. Exogenous melatonin alleviates cadmium-induced inhibition of growth and photosynthesis through upregulating antioxidant defense system in strawberry. S Afr J Bot. 2023;157:10–8.

Shah HMS, Singh Z, Hasan MU, Afrifa-Yamoah E, Woodward A. Preharvest melatonin application alleviates red drupelet reversion, improves antioxidant potential and maintains postharvest quality of 'Elvira'blackberry. Postharvest Biol Technol. 2023;203: 112418.

Shang F, Liu R, Wu W, Han Y, Fang X, Chen H, Gao H. Effects of melatonin on the components, quality and antioxidant activities of blueberry fruits. Lwt. 2021;147: 111582.

Shao R, Wang Y, He C, Chen L. Melatonin and its emerging physiological role in reproduction: a review and update. Curr Mol Med. 2024;24:449–56.

Sharafi Y, Jannatizadeh A, Fard JR, Aghdam MS. Melatonin treatment delays senescence and improves antioxidant potential of sweet cherry fruits during cold storage. Sci Hortic. 2021;288: 110304.

Sharma SK, Sharma I, Bhushan B. A review of melatonin metabolism with reference to plants. Int J Adv Res Biol Sci. 2023;10(9):1–10.

Shen T, Liang D, Wang X, Lv X, Wang J, Xia H. Effect of Melatonin on the Breaking Dormancy of Kiwifruit Seeds. In: IOP conference series: earth and environmental science, vol. 237, No. 5, p. 052073. IOP Publishing; 2019.

Sun C, Huang Y, Lian S, Saleem M, Li B, Wang C. Improving the biocontrol efficacy of Meyerozyma guilliermondii Y-1 with melatonin against postharvest gray mold in apple fruit. Postharvest Biol Technol. 2021a;171: 111351.

Sun C, Liu L, Wang L, Li B, Jin C, Lin X. Melatonin: a master regulator of plant development and stress responses. J Integr Plant Biol. 2021b;63(1):126–45.

Suresh TR, Pradhan J, Kumar S, Singh H, Prasad K, Jaiswal A, Kumari G. Melatonin discovery and divergent biosynthetic pathways in plants. In: Melatonin in plants: a regulator for plant growth and development. Springer Nature Singapore: Singapore; 2023. p. 1–18.

Tan DX, Reiter RJ. An evolutionary view of melatonin synthesis and metabolism related to its biological functions in plants. J Exp Bot. 2020;71(16):4677–89.

Tang Q, Li C, Ge Y, Li X, Cheng Y., Hou J, & Li J. Exogenous application of melatonin maintains storage quality of jujubes by enhancing anti-oxidative ability and suppressing the activity of cell wall-degrading enzymes. Lwt. 2020;127:109431.

Tijero V, Munoz P, Munne-Bosch S. Melatonin as an inhibitor of sweet cherries ripening in orchard trees. Plant Physiol Biochem. 2019;140:88–95.

Tiwari RK, Lal MK, Naga KC, Kumar R, Chourasia KN, Subhash S, et al. Emerging roles of melatonin in mitigating abiotic and biotic stresses of horticultural crops. Sci Hortic. 2020;272: 109592.

Tiwari RK, Lal MK, Kumar R, Chourasia KN, Naga KC, Kumar D, et al. Mechanistic insights on melatonin-mediated drought stress mitigation in plants. Physiol Plant. 2021a;172(2):1212–26.

Tiwari RK, Lal MK, Kumar R, Mangal V, Altaf MA, Sharma S, et al. Insight into melatonin-mediated response and signaling in the regulation of plant defense under biotic stress. Plant Mol Biol. 2021b;109:1–15.

Tiwari RK, Altaf MA, Kumar R, Lal MK. Evolution of melatonin as an oxidative stress mitigator in plant. In: Melatonin in plants: a pleiotropic molecule for abiotic stresses and pathogen infection. Springer Nature Singapore: Singapore; 2024. p. 1–20.

Tyczewska A, Woźniak E, Gracz J, Kuczyński J, Twardowski T. Towards food security: current state and future prospects of agrobiotechnology. Trends Biotechnol. 2018;36(12):1219–29.

Uğur Y. Extraction and quantification of melatonin in cornelian cherry (*Cornus mas* L.) by ultra-fast liquid chromatography coupled to fluorescence detector (UFLC-FD). Acta Chromatogr. 2023;35(3):219–26.

Umamaheswari R, Prasannakumar NR, Sriram S, Sharma SK, Rao MS, Chaya MK. Biotic stress management in horticultural crops using microbial intervention. In: Rhizosphere microbes: soil and plant functions. Springer; 2020. p. 619–54.

Usanmaz S, Aşkın MA, Kahramanoğlu İ. Effects of foliar melatonin application on the flowering and fruit set of pomegranate (*Punica granatum* L. Wonderful). In: V international symposium on pomegranate and minor mediterranean fruits. 2022; 1349. p. 63–72.

Varma S, Jangra M. Heavy metals stress and defense strategies in plants: An overview. J Pharmacognosy Phytochem. 2021;10(1):608–14.

Verde A, Míguez JM, Gallardo M. Melatonin and related bioactive compounds in commercialized date palm fruits (*Phoenix dactylifera* L.): correlation with some antioxidant parameters. Eur Food Res Technol. 2019;245:51–9.

Verde A, Míguez JM, Leao-Martins JM, Gago-Martínez A, Gallardo M. Melatonin content in walnuts and other commercial nuts Influence of cultivar, ripening and processing (roasting). J Food Compos Anal. 2022a;105: 104180.

Verde A, Míguez JM, Gallardo M. Role of melatonin in apple fruit during growth and ripening: possible interaction with ethylene. Plants. 2022b;11(5):688.

Wang F, Zhang X, Yang Q, Zhao Q. Exogenous melatonin delays postharvest fruit senescence and maintains the quality of sweet cherries. Food Chem. 2019;301: 125311.

Wang L, Luo Z, Yang M, Li D, Qi M, Xu Y, et al. Role of exogenous melatonin in table grapes: first evidence on contribution to the phenolics-oriented response. Food Chem. 2020b;329: 127155.

Wang Y, Wang G, Xu W, Zhang Z, Sun X, Zhang S. Exogenous melatonin improves pear resistance to *Botryosphaeria dothidea* by increasing autophagic activity and sugar/organic acid levels. Phytopathology®. 2022a;112(6):1335–44.

Wang K, Xing Q, Ahammed GJ, Zhou J. Functions and prospects of melatonin in plant growth, yield, and quality. J Exp Bot. 2022b;73(17):5928–46.

Wang M, Li Y, Li C, Xu H, Sun T, Ge Y. Melatonin induces resistance against *Penicillium expansum* in apple fruit through enhancing phenylpropanoid metabolism. Physiol Mol Plant Pathol. 2023;127: 102082.

Wei J, Liang J, Liu D, Liu Y, Liu G, Wei S. Melatonin-induced physiology and transcriptome changes in banana seedlings under salt stress conditions. Front Plant Sci. 2022;13: 938262.

Wijesinghe P, Wijeweera G, De Silva KRD. Healthy brain ageing and longevity; the harmony of natural products, APOE polymorphism, and melatonin. In: Sleep and clocks in aging and longevity. Cham: Springer International Publishing; 2023. p. 143–64.

Wu S, Wang Y, Zhang J, Gong X, Zhang Z, Sun J, et al. Exogenous melatonin improves physiological characteristics and promotes growth of strawberry seedlings under cadmium stress. Horticult Plant J. 2021a;7(1):13–22.

Wu X, Ren J, Huang X, Zheng X, Tian Y, Shi L, et al. Melatonin: biosynthesis, content, and function in horticultural plants and potential application. Sci Hortic. 2021b;288: 110392.

Wu C, Hao W, Yan L, Zhang H, Zhang J, Liu C, Zheng L. Postharvest melatonin treatment enhanced antioxidant activity and promoted GABA biosynthesis in yellow-flesh peach. Food Chem. 2023;419: 136088.

Xia H, Zhou Y, Deng H, Lin L, Deng Q, Wang J, et al. Melatonin improves heat tolerance in *Actinidia deliciosa* via carotenoid biosynthesis and heat shock proteins expression. Physiol Plant. 2021a;172(3):1582–93.

Xu L, Yue Q, Xiang G, Bian FE, Yao Y. Melatonin promotes ripening of grape berry via increasing the levels of ABA, H2O2, and particularly ethylene. Horticult Res. 2018;5:41.

Yılmaz UĞUR. Investigation of Melatonin content and antioxidant capacity in grape berries. İnönü Üniversitesi Sağlık Hizmetleri Meslek Yüksek Okulu Dergisi. 2021;9(3):820–30.

Zahedi SM, Hosseini MS, Abadía J, Marjani M. Melatonin foliar sprays elicit salinity stress tolerance and enhance fruit yield and quality in strawberry (*Fragaria*× *ananassa* Duch.). Plant Physiol Biochem. 2020;149:313–23.

Zahra N, Shaukat K, Hafeez MB, Raza A, Hussain S, Chaudhary MT, et al. Physiological and molecular responses to high, chilling, and freezing temperature in plant growth and production: consequences and mitigation possibilities. In: Harsh environment and plant resilience: molecular and functional aspects. Springer; 2021. p. 235–90.

Zhang H, Liu X, Chen T, Ji Y, Shi K, Wang L, et al. Melatonin in apples and juice: Inhibition of browning and microorganism growth in apple juice. Molecules. 2018;23(3):521.

Zhang H, Wang L, Shi K, Shan D, Zhu Y, Wang C, et al. Apple tree flowering is mediated by low level of melatonin under the regulation of seasonal light signal. J Pineal Res. 2019a;66(2): e12551.

Zhang Y, Gong Y, Chen L, Peng Y, Wang Q, Shi J. Hypotaurine delays senescence of peach fruit by regulating reactive oxygen species metabolism. Sci Hortic. 2019b;253:295–302.

Zhang Z, Wang T, Liu G, Hu M, Yun Z, Duan X, et al. Inhibition of downy blight and enhancement of resistance in litchi fruit by postharvest application of melatonin. Food Chem. 2021;347: 129009.
Zhang L, Yu Y, Chang L, Wang X, Zhang S. Melatonin enhanced the disease resistance by regulating reactive oxygen species metabolism in post-harvest jujube fruit. J Food Process Preserv. 2022a;46(3): e16363.
Zhang T, Wang J, Sun Y, Zhang L, Zheng S. Versatile roles of melatonin in growth and stress tolerance in plants. J Plant Growth Regul. 2022b;41:1–17.
Zhang Y, Tang H, Lei D, Zhao B, Zhou X, Yao W, et al. Exogenous melatonin maintains postharvest quality in kiwiberry fruit by regulating sugar metabolism during cold storage. LWT. 2023;174: 114385.
Zhao D, Yu Y, Shen Y, Liu Q, Zhao Z, Sharma R, Reiter RJ. Melatonin synthesis and function: evolutionary history in animals and plants. Front Endocrinol. 2019;10:249.
Zhu W, Cao H, Wang Q, Niu Y, Sadeghnezhad E, Han S, et al. Transcriptome analysis revealed MAPK and hormone pathway involving in exogenous melatonin-regulated salt tolerance in sour jujube. Fruit Res. 2023;3(1):19.

Publisher's Note