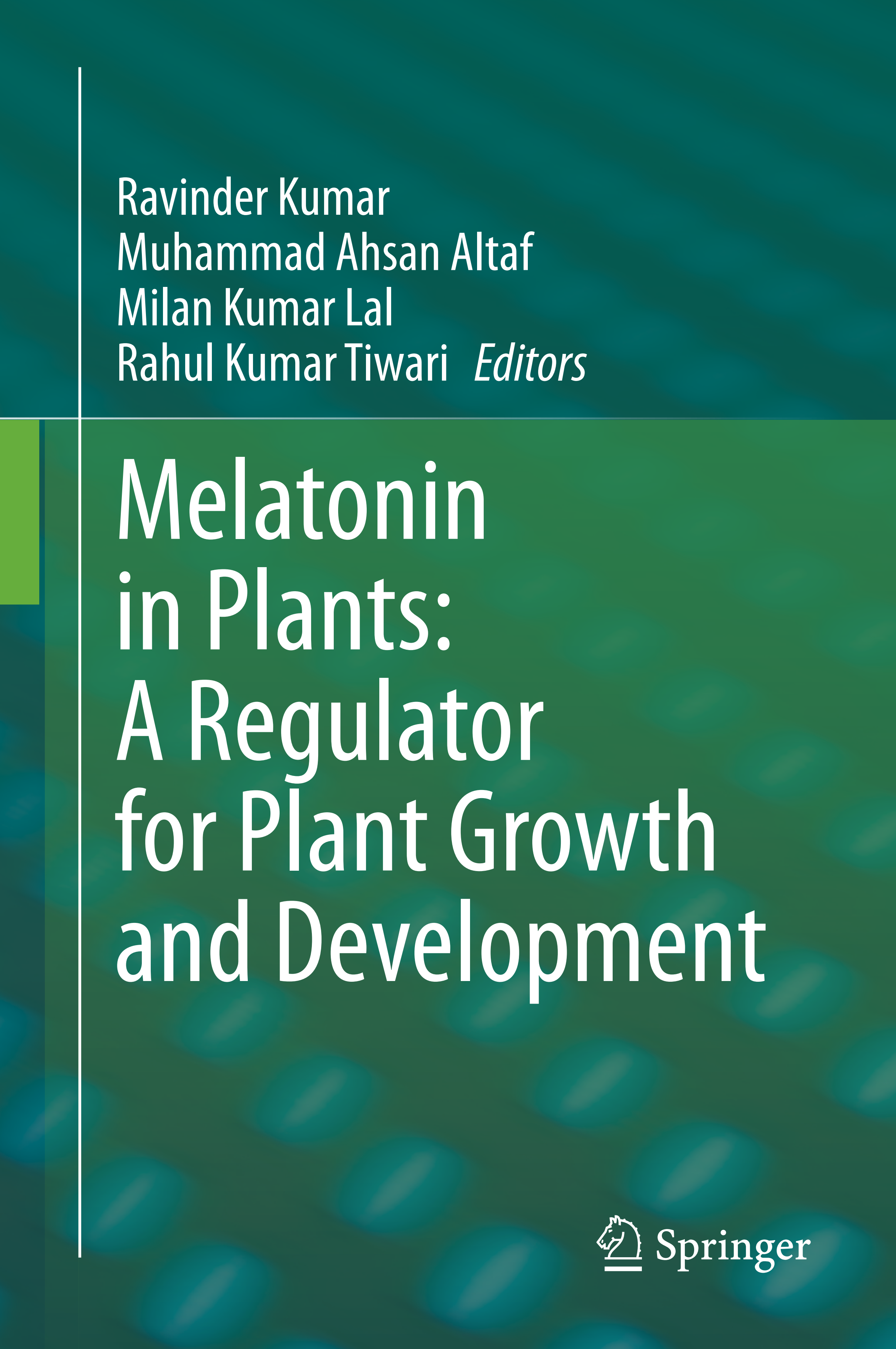

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Melatonin in Plants: A Regulator for Plant Growth and Development

Springer

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Preface

The concept of melatonin as a ubiquitous and multifunctional molecule in the biological systems of organisms has undergone a profound transformation in recent years. Melatonin was initially known for its ability to regulate circadian rhythms in animals, but its significance and presence in plant biology has emerged as a fascinating and rapidly developing research field. These discoveries have led to a scientific renaissance, resulting in a better understanding of melatonin's pleiotropic effects on diverse physiological processes.

The book entitled *Melatonin in Plants: A Regulator for Plant Growth and Development* aims to illuminate melatonin's role in plant growth and development in an enigmatic manner. A number of eminent researchers and scientists have investigated and pursued the intricacies of melatonin's role in plant physiology, and the chapters presented here are the result of their research. A primary objective of this compendium is to provide a comprehensive overview of melatonin's role in regulating plant growth, development, and responses to environmental factors. Melatonin biology is explored in each chapter, including biosynthesis, signaling pathways, and interactions with other plant hormones. As a key mediator in enhancing plant resilience to adverse conditions, melatonin also plays an important role in the book's exploration of the crossroads between abiotic stresses and melatonin.

Increasing global population and climate change have made it increasingly urgent to understand the mechanisms that govern plant responses to environmental changes in recent years. The chapters within this volume illustrate how melatonin optimizes plant survival, acclimation, and adaptation in the face of abiotic stresses, such as drought, salinity, extreme temperatures, and heavy metal toxicity. It also discusses the intricate interplay between plant-pathogen interactions and melatonin. Melatonin plays a crucial role in enhancing plant immunity and defense mechanisms, as plant diseases and pathogens pose significant threats to global food security.

As we embark on this journey through the evolving landscape of melatonin research in plants, we invite readers to immerse themselves in the diverse array of topics, methodologies, and perspectives presented herein. In this compendium, melatonin is explored in light of its remarkable versatility in orchestrating the intricate ballet of plant growth and development.

Our heartfelt gratitude goes out to the contributors, whose dedication, expertise, and passion have culminated in this illuminating book. Their collective efforts have enriched our understanding of the critical role played by melatonin in shaping the destiny of plants, as they navigate the dynamic interplay of environmental cues and intrinsic physiological responses. In addition to serving as a valuable resource for students, researchers, and practitioners in plant biology, agriculture, and the environment, we hope this book will inspire new avenues of inquiry and drive innovative applications, ensuring a sustainable future for our planet by harnessing the potential of melatonin.

New Delhi, India	Ravinder Kumar
Sanya, China	Muhammad Ahsan Altaf
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Ravinder Kumar Ph.D., Senior Scientist (Plant Pathology), ICAR-Central Potato Research Institute, Shimla, Himachal Pradesh, India, has over 15 years of research experience in biotic and abiotic stress management in plants, potato biotechnology particularly formulation of dsRNA for late blight, development of transgenic lines with ToLCNDV resistance, potato genetic resource management, and the development of several diagnostic tools like uniplex/multiplex RT-PCR, real-time RT-PCR, LAMP, and RT-RPA protocols for detecting potato pathogens, molecular characterization and genome sequencing of plant pathogens. He has published over 120 research papers/review articles in national/international peer-reviewed journals, training manuals, and book chapters and edited institute publications like newsletters and annual reports. He is the recipient of awards like IPA-Kaushalya Sikka Memorial Award, IPA-Chandra Prabha Singh Young Scientist Award, Young Scientist Associate award, and best oral/poster awards of different scientific professional societies. He is also a member of the editorial board for ten international journals and serves as a guest associate editor for several reputed international journals.

Muhammad Ahsan Altaf earned his Ph.D. from the School of Life Science at Hainan University in China. Following that, he completed his post-doctoral studies at the School of Horticulture, also at Hainan University. Currently, he holds the position of Scientific Researcher at the School of Breeding and Multiplication, Sanya Institute of Breeding and Multiplication (Hainan University, Sanya, China). Throughout his career, Dr. Altaf has contributed significantly to the field of horticultural research. He has authored more than 90 research articles, which have been published in esteemed international journals with high impact factors. His research interests predominantly revolve around the physiological, biochemical, and molecular aspects of horticultural plants. Specifically, he is deeply involved in exploring the role of melatonin in enhancing photosynthetic efficiency and facilitating mineral nutrient uptake, from the roots to the shoots of these plants, especially under challenging abiotic stress conditions.

Milan Kumar Lal, Doctor in Plant Physiology, works in the area of abiotic stress and the nutritional aspects of potato and other starchy crops at ICAR-Central Potato Research Institute, Shimla, India. He is an expert worker in the area of abiotic stress such as heat, drought salinity, and heavy metal. Moreover, he is also working on the aspect of effect of biotic stress such as fungus, virus, and bacteria on plant physiological, biochemical, and molecular responses. Apart from this, he also has expertise in the nutritional and quality aspects of starchy crops, including resistant starch, glycemic index, phytonutrients, functional fermented foods and beverages, bioactive compounds, and various processing techniques to enhance these components in food products of starchy crops. He is the recipient of prestigious awards such as the Best PhD Thesis Award, PhD Merit Medal Award, Young Researcher Award, and RD Asana Gold Medal Award. His findings have generated more than 120 publications in international peer-reviewed journals.

Rahul Kumar Tiwari, Doctor in Plant Pathology, works as a scientist at ICAR-Central Potato Research Institute Shimla, India. The research work of Dr Tiwari is focused on the management of crop diseases, abiotic stress mitigation in horticultural crops, and the role of phytohormones in plant defense. His recent research findings on the impact of Fusarium dry rot disease on potatoes provide critical information on the pathogen, its genomics, and potential management strategies. Moreover, Dr Tiwari's research on the development of one-step reverse transcription recombinase polymerase amplification (RT-RPA) assays for the detection of potato viruses has the potential to contribute significantly to the development of disease-free potato seed certification programs. Dr Rahul Kumar Tiwari's exceptional research work has been widely recognized and awarded, including the IARI Gold Medal Award for his outstanding Ph.D. research work and the Young Scientist Award. He has authored over 80 publications in highly acclaimed international and national peer-reviewed journals, book chapters, newsletters, and popular articles.

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Abbreviations

AADC	Aromatic amino acid decarboxylase
AANAT	Aralkylamine *N*-acetyltransferase
ABA	Abscisic acid
AIs	Adenylate isopentenyltransferases
AMK	N^1-acetyl-5-methoxykynuramine
ANS	Anthocyanidin synthase
APA	American Psychiatric Association
APX	Ascorbate peroxidase
ASMT	Acetylserotonin *O*-methyltransferase
BRs	Brassinosteroids
CAGR	Compound annual growth rate
CAS	Cyanoalanine synthase
CAT	Catalase
CBFs	C-repeat-binding factors
CCA1	Circadian Clock-Associated 1
CHI	Chalcone isomerase
CHS	Chalcone synthase
COMT	Caffeic acid *O*-methyltransferase
COR	Cold-responsive genes
COX-2	Cyclooxygenase-2
CRY1	Cryptochrome 1
CWIN	Cell wall invertase
DAHP	3-Deoxy-D-arabino-heptulosonate-7-phosphate
DCD	D-Cysteine desulfhydrase
DFR	Dihydroflavonol reductase
DHAR	Dehydroascorbate reductase
DHQ	3-Dehydroquinic acid
DHS	3-Dehydroshikimate
ECHA	European Chemicals Agency
EL	Electrolyte leakage
EPSP	5-Enolpyruvylshikimate-3-phosphate
ETC	Electron transport chain
F3H	Flavanone 3-hydroxylase

GADPH	Glyceraldehyde 3-phosphate dehydrogenase
GAs	Gibberellins
GB	Glycine betaine
GC-MS	Gas chromatography-mass spectrometry
GGDP	Geranylgeranyl diphosphate
GPOX	Guaiacol peroxidase
GPX	Glutathione peroxidase
GPXL	Glutathione peroxidase-like
GR	Glutathione reductase
GSNO	*S*-nitrosoglutathione
H_2S	Hydrogen sulfide
HIOMT	Hydroxyindole-*O*-methyltransferase
HSPs	Heat shock proteins
IAA	Indole-3-acetic acid
IAM	Indole-3-acetamide
IAOx	Indole-3-acetaldoxime
iPMP	Isopentenyladenosine 5′-monophosphate
IPP	Isopentenyl diphosphate
IPTs	Isopentenyltransferases
IPyA	Indole-3-pyruvic acid
LCD	L-cysteine desulfhydrase
LC-MS	Low-cost mass spectrometry
LHY	Late elongated hypocotyl
MAE	Microwave-assisted extraction
MAP	Modified atmosphere packaging
MAPKs	Mitogen-activated protein kinases
MDA	Malondialdehyde
MDHAR	Monodehydroascorbate reductase
MeJA	Methyl jasmonate
MEPS	Microextraction by packed sorbent
MET	Metallothioneins
MSH	Melanocyte-stimulating hormone
MV	Methyl viologen
NADPH	Nicotinamide adenine dinucleotide phosphate
NAS	*N*-acetylserotonin
NAT	*N*-acetyltransferase
NO	Nitric oxide
NTFP	Non-timber forest products
PAL	Phenylalanine ammonia-lyase
PAMPs	Pathogen-associated molecular patterns
PCs	Phytochelatins
PEP	2-Phosphoenolpyruvate
PEPC	Enzyme phosphoenolpyruvate carboxylase
PRA	Phosphoribosyl anthranilate
PRAI	PRA isomerase

PRPP	Phosphoribosylpyrophosphate
RBOHs	Respiratory burst oxidase homologs
RIA	Radioimmunoassay
RNS	Reactive nitrogen species
ROS	Reactive oxygen species
SAM	*S*-adenosylmethionine
SiR	Sulfite reductase
SNAT	Serotonin *N*-acetyltransferase
SNMT	Serotonin *N*-methyltransferase
SOD	Superoxide dismutase
SPF	Spray polyurethane foam
SUSY	Sucrose synthase
T5H	Tryptamine-5-hydroxylase
TAM	Tryptamine
TDC	Tryptophan decarboxylase
TPH	Tryptophan hydroxylase
TPS	Tryptophan synthase
XOR	Xanthine oxidoreductase

1 Melatonin Discovery and Divergent Biosynthetic Pathways in Plants

Thakur Roshan Suresh, Jyostnarani Pradhan, Shailesh Kumar,
Hemlata Singh, Killi Prasad, Aman Jaiswal, and Geeta Kumari

Abstract

Despite the fact that we all know that melatonin plays a role and has some profound effects on animals, recent studies have shown that this biochemical can also be found in plants, microorganisms, and algae, and its effects can be seen in these organisms as well. Primarily, melatonin is considered a “sleep hormone”. In animals, it acts as an antioxidant, anti-inflammatory, and anti-carcinogenic agent and is used to treat several diseases. It is available in the market as a supplement. Melatonin has several functional roles in the plants, such as abiotic stress tolerance, as a secondary metabolite, synthesis of several phytohormones, defence mechanism, acts as a phytohormone, seedling growth, fruit development, root development, seed germination, flower development, crop and fruit yield, fruit storage, etc. Melatonin acts differently in different growth phases of the plants, viz., vegetative and reproductive phases. Also, it is found to have nutraceutical value. Here, in this chapter, we are dealing briefly with a historical perspective of this hormone, the isolation of this compound, how this hormone has importance in animals as well as in plants, how it was discovered, its biosynthetic pathways, the precursors and organelles involved in synthesis; altogether. Also, we are dealing with the comparative study of the mechanism

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of this newly discovered chemical in plants as well as animals, along with its current use in our day-to-day lives. Various studies have shown the abundance of this molecule and its benefits for humankind and plants.

Keywords

Melatonin · Plants · Animals · Biosynthetic pathways · Nutraceutical value

1.1 Introduction

Melatonin has also been studied for use in treating sleep disorders in addition to jet lag. Generally speaking, it decreases sleep latency and enhances sleep, particularly when circadian phasing is disrupted. Patients with neurological illnesses benefited the most from this in the latter situation (Hardeland 2005; Altaf et al. 2023). Several initiatives designed to lessen the effects of neurodegenerative illnesses such as Alzheimer's disease, Parkinson's disease, Huntington's disease, and amyotrophic lateral sclerosis have been created or are being investigated to deal with these conditions (Altaf et al. 2022a, b). The effectiveness of this compound as a cancer-fighting agent has been extensively studied. More research should be focused on the potential anti-inflammatory effects of N^1-acetyl-5-methoxykynuramine (AMK), particularly given that AMK is a natural downregulation and inhibitor of COX-2 (cyclooxygenase-2) (Hardeland 2005). The regulation of melatonin in the sleep/ wake cycle, seasonal rhythms, and other circadian rhythms has already been observed, as well as its effect as an immunostimulator and cytoprotective agent. It has been observed that the substance is capable of safeguarding mitochondrial electron flux, antioxidant protection, and neuroprotection in various experimental systems. At night, melatonin levels are more significantly elevated, then information about "darkness" is passed on to the brain and light suppresses the mechanism by which it increases (Hardeland et al. 2006).

The chemical compound N-acetyl-5-methoxytryptamine, also referred to as melatonin, has been extensively researched in other parts of the world, and it is found in all living organisms, i.e., it is everywhere (Lerner et al. 1958; Zhang et al. 2023). In addition, it has been identified as a plant hormone that plays an important role in facilitating the regulation and development of plants (Arnao and Hernández-Ruiz 2019). A number of studies have shown that melatonin plays an essential role in maintaining a healthy circadian rhythm, sleep, mood, body temperature, appetite, and immune response in humans (Socaciu et al. 2020). Melatonin is a common indolamine that has received much research because the substance plays an essential role in controlling a wide range of physiological processes in animals and plants (Fig. 1.1). During the twentieth century, scientists discovered that certain plant species can synthesize large quantities of this chemical and store it in specialized tissues throughout the plant. As a result, it has been considered a ubiquitous molecule (Mannino et al. 2021).

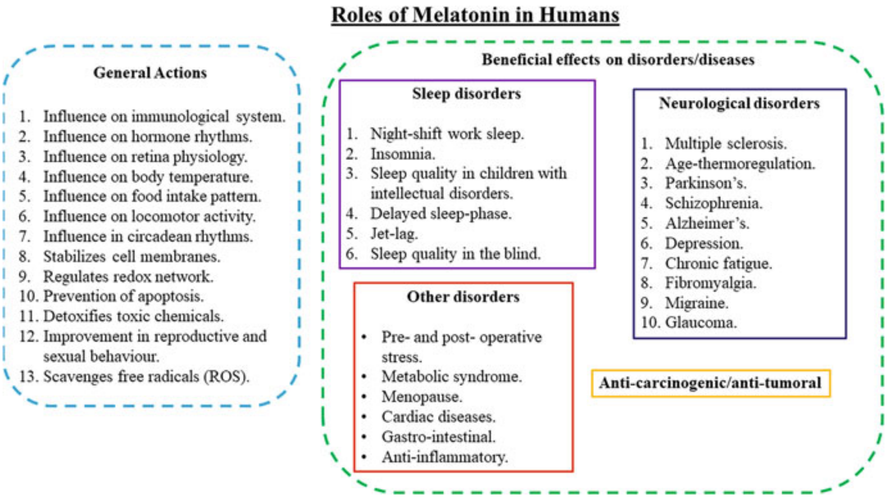

Fig. 1.1 Roles of melatonin in human physiology. Melatonin serves as a beneficial molecule/chemical in humans. Several functions of this hormone are depicted here entitled general actions, beneficial effects on sleep disorders, neurological disorders, other disorders, and anti-carcinogenic/anti-tumoral effects. *ROS* reactive oxygen species

It was originally thought that, when the substance was discovered, it was an antioxidant that had a wide range of positive effects on the various phases of plant growth and development, such as germination, root extension, photosynthesis, and leaf senescence (Arnao and Hernández-Ruiz 2019), as well as photosynthesis and leaf senescence (Wang et al. 2022). Among the many bioactive compounds present in vascular plants, it has been observed to be one of the most important (Ahmad et al. 2023) The compound can be found in a wide range of plant tissues, including those of seeds, roots, leaves, and fruits (Ahmad et al. 2023) Melatonin has been used extensively for disease pathogenesis and therapeutic development since it has been shown to modulate antioxidant, anti-inflammatory, and other biological properties (Zhang et al. 2023).

Melatonin is an artificially manufactured form of hormone present in animals, bacteria, plants, and fungi; apart from its antioxidant properties, melatonin has applications in beverages and food, dietary supplements, and pharmaceuticals. Bio-based "SPF" (spray polyurethane foam) is also synthesized from melatonin and having a role in generating insulation (Market analysis report 2019–2025). It is suggested by APA (American Psychiatric Association) reports that, throughout their lives, about one-third of adults experience sleep problems i.e., insomnia. Symptoms of this are persistent difficulties falling and persist in being asleep. Hence, it is obvious to observe the increased use of artificially synthesized melatonin (Lal et al. 2022; Mishra et al. 2022; Naz et al. 2022). It is expected that over the next 5 years, according to calculations, the Compound Annual Growth Rate (CAGR) for the melatonin market will be greater than 10%. The major companies which are functional in Melatonin Market are, viz., LLC, Natrol, Aspen Holdings, Pfizer

Incorporation, Biotics Research Corporation, Nature's Bounty (Market analysis report 2019–2025; Mordor Intelligence 2023–2028).

1.2 Melatonin Discovery in Animals and Plants

Up until 1995, "melatonin" had been one of the compounds that had received the most attention in the scientific literature as well as specialized journals, such as the Melatonin Research and Journal of Pineal Research (founded in 1984), which was founded in 1985. There was a belief that an animal hormone might be the cause of this problem in particular. However, after that, the undeniable discovery of plant-based melatonin was eventually made available to the scientific community back in 1995 by a trio of different research groups (Hattori et al. 1995; Dubbels et al. 1995). Similarly, Dr. Saxena's group in Canada has been developing and carrying out a line of research that is of particular interest. Various studies have suggested that melatonin may function as an auxin in in vitro cell cultures as a result of the structural similarities between IAA (indole-3-acetic acid) and melatonin. The researchers discovered phases of the phytomelatonin production pathway that were identical to the pathways already present in mammals (Murch et al. 2000, 2001; Murch and Saxena 2002) while they were studying the cells of St. John's wort (*Hypericum perforatum* L.) culture.

There was an initial confirmation in 2004 that melatonin had a growth-stimulating effect in the hypocotyls of etiolated lupin (*Lupinus albus* L.), with an estimated stimulatory potential up to 63% when compared to IAA's effects on lupin (Hernández-Ruiz et al. 2004). As previously mentioned, melatonin is the scientific name given to a hormone that is able to contract melanophores, which is implicated in the lightening of skin in frogs and fish melanocytes (skin-lightening molecule) (Hardeland et al. 2006). As a matter of fact, melatonin is now well known to exist in all kingdoms of life, from prokaryotes to eukaryotes, and even in plants (Lal et al. 2023; Kumar et al. 2023a, b). Phytomelatonin is the name given to a molecule that can be found in plants, known as melatonin (Arnao 2014). There is a distinction between phytomelatonin, which is derived from algae and plants, and animal or synthetic melatonin, which is derived from animals or synthetic materials. There are a number of studies that deal with plant-derived melatonin, such as those in food chemistry, plant physiology, phytochemistry, botany, and so on, but this term is often used in these studies. A pleiotropic chemical that has many roles in a variety of physiological reactions in plants is phytomelatonin (Arnao and Hernández-Ruiz 2018, 2020a, 2022; Aghdam et al. 2022).

This hormone, originally discovered as a hormone produced by the pineal gland of a cow (Lerner et al. 1958; Arnao and Hernández-Ruiz 2020b), is now produced by fungi, invertebrates, protozoa, bacteria, plants, the Harderian gland, skin, gut, leukocytes, and a number of extrapineal sites in vertebrates. As a result of the accumulation of melanin granules in the melanocytes, this active factor plays a crucial role in illuminating the skin colour of tadpoles, frogs, toads, and some fish, but does not affect animals (Fig. 1.2). Melatonin is the name of the compound, and it

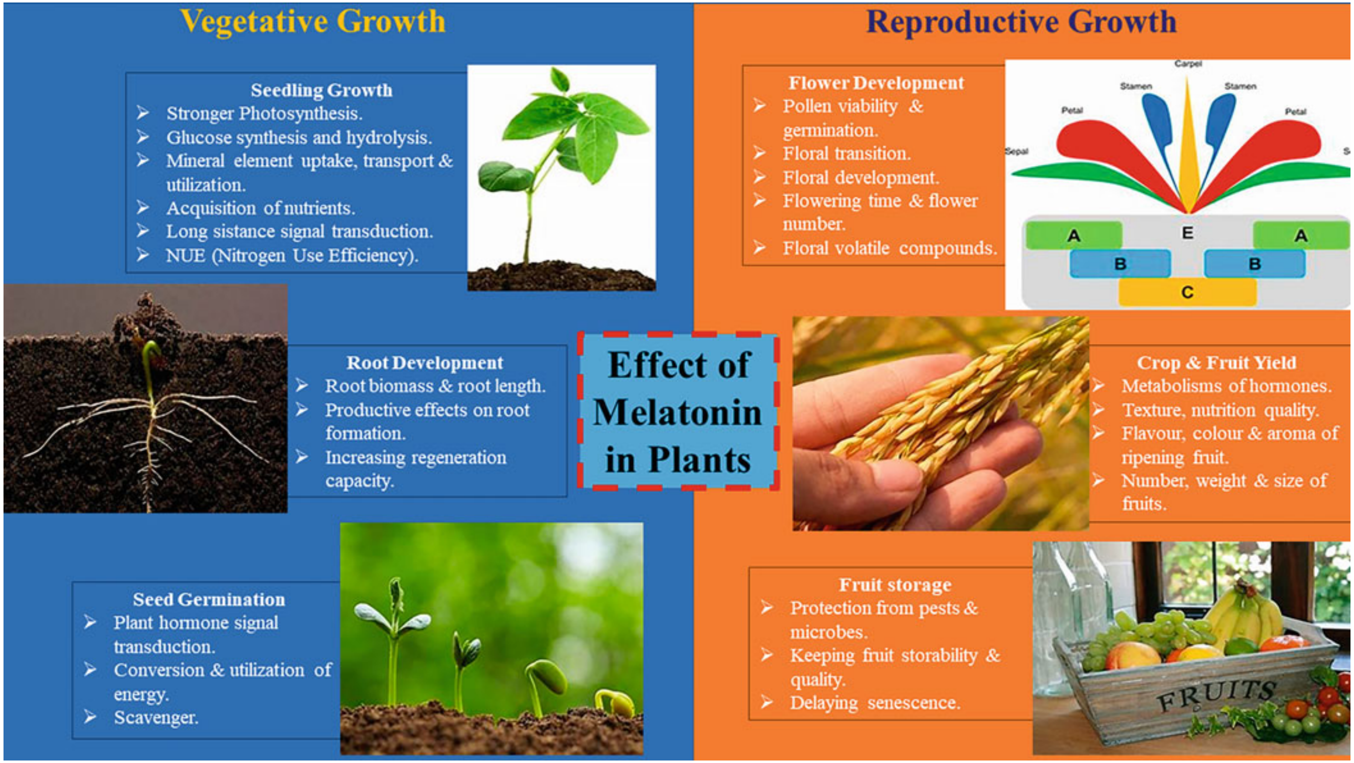

Fig. 1.2 This figure illustrates the effects of melatonin on plant growth and development, including seed germination, root development, seedling growth, flower development, crop and fruit yield, and fruit storage, which are all important in the development and growth of plants. (Modified from Zhang et al. 2023)

was scientifically identified as a N-acetylserotonin derivative in 1959 by Arnao and Hernández-Ruiz (Arnao and Hernández-Ruiz 2020a).

In 1960, Lerner isolated and identified this compound as a small molecule with a molecular weight of 232 Daltons. It was discovered that this molecule aggregated pigment granules in both fish and frog skin; hence, it was named. Melatonin is an extensively dispersed chemical found in all kingdoms of life (Mannino et al. 2021; Arnao et al. 2022). There are several physiological properties of melatonin that contribute to its ability to combat oxidative stress, promote reproduction, and promote plant growth. Plant NPs (natural products) are considered to be hormones as well as plant hormones (Mangal et al. 2023; Watpade et al. 2023). In an indirect manner, melatonin is synthesized through the shikimate pathway, as it is a by-product of the shikimate pathway (Elshafie et al. 2023). Including its pleiotropic properties, melatonin is an important abiotic stress signalling molecule for plants as it makes them more resilient to both mild and severe conditions, and it affects many aspects of their development and function (Ahmad et al. 2023).

1.3 Melatonin Precursors and Organelle Involved

Melatonin was discovered to be a component of all vertebrates, to be rhythmically modulated by the pineal gland's secretion, and to have a role in the circadian control and, occasionally, in the seasonal patterns (Hardeland et al. 2006). Several subcellular compartments, including the cytoplasm, endoplasmic reticulum, mitochondria, and chloroplasts, synthesize melatonin intermediates that control the following enzymatic pathways (Zhao et al. 2019; Arnao et al. 2023). It has been shown that rice plants contain up to four genes for histone DAC (deacetylases), enzymes that may reverse the conversions of 5-methoxytryptamine and serotonin into N-acetylserotonin and melatonin, respectively. Deacetylase activity of DAC is maximum for N-acetyltyramine. Also, the chloroplast-expressed DAC displayed enzyme activity towards melatonin, N-acetyltryptamine, and N-acetylserotonin (Lee et al. 2018; Arnao et al. 2023).

The PMTR1, phytomelatonin receptor facilitates ROS signalling, controls homeostasis, and transmits a dark signal that stimulates night stomatal closure (preventing water loss during the night), which aids plant adaptation to dryland environments (Li et al. 2020). Melatonin is a multiregulatory molecule that controls the expression of genes related to abiotic stress resistance, the redox reactions and plant growth and development, sucrose metabolism {CWIN [cell wall invertase] and SUSY [sucrose synthase]}, and specialized metabolism {phenylpropanoid metabolism: DFR [dihydroflavonol reductase], CHI [chalcone isomerase] (Fig. 1.3). PAL [phenylalanine ammonia lyase], F3H [flavanone 3-hydroxylase], CHS [chalcone synthase], and ANS [anthocyanidin synthase]} (Weeda et al. 2014; Ahmad et al. 2023).

In plant cells, the location of the enzymes involved in the production of melatonin from tryptophan is varied. TDC is contained in the cytoplasm (Zhou et al. 2020). In chloroplasts, SNAT is expressed; in the endoplasmic reticulum, T5H is expressed

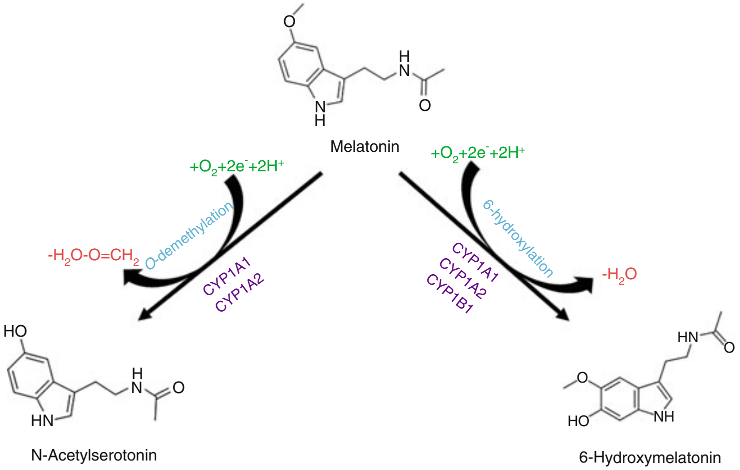

Fig. 1.3 The different P450 isozymes react with melatonin in different ways. For example, CYP1A1, CYP1A2, and CYP1B1 cause dominant 6-hydroxylation, but CYP2C19 creates products of the *O*-demethylation only in certain circumstances. However, some products of the *O*-demethylation are also seen with CYP1A2

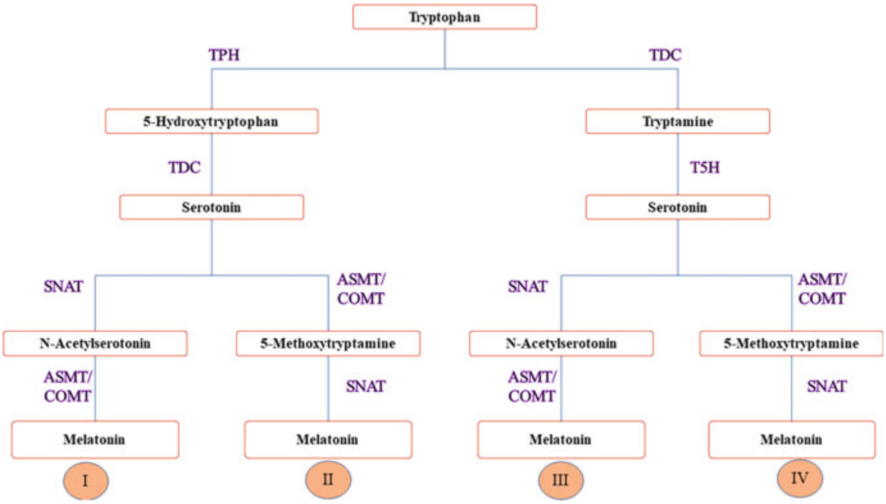

Fig. 1.4 Simplified representation of the melatonin biosynthesis via four different pathways. *TPH* tryptophan hydroxylase, *TDC* L-tryptophan decarboxylase, *T5H* tryptamine-5-hydroxylase, *SNAT* serotonin *N*-acetyltransferase, *ASMT* acetylserotonin *O*-methyltransferase, *COMT* caffeic acid 3-*O*-methyltransferase

(Back 2021; Rather et al. 2022), ASMT and COMT, however, are found in the cytoplasm (Mannino et al. 2021). The first and second of the four probable biosynthetic pathways of melatonin shown in Fig. 1.4 occur in the cytoplasm, while the third and fourth pathways lead to serotonin production in the endoplasmic reticulum (Back et al. 2016). Melatonin synthesis and accumulation can occur at a variety of ultimate subcellular sites; however, SNATs are exclusively found in the chloroplast and ASMTs/COMT in the cytoplasm. For instance, the serotonin SHT (N-hydroxycinnamoyl transferase) rapidly converts serotonin into phenylpropanoid amides in the cytoplasm, such as feruloylserotonin (Byeon and Back 2015). 2-OHM (2-hydroxymelatonin) is a product of the melatonin metabolism in chloroplasts; this reaction is catalysed by M2H (melatonin-2-hydroxylase). Conversely, melatonin is quickly transformed into cyclic 3-OHM (3-hydroxymelatonin) by M3H (melatonin-3-hydroxylase) (Lee et al. 2016; Ye et al. 2019).

1.4 Melatonin Biosynthetic Pathway in Animals and Plants

All vertebrates now have an enlarged mechanism for melatonin production, and other creatures, like insects, can also use this system (Herbert et al. 1960; Rahman et al. 2023; Thakur et al. 2023; Bairwa et al. 2023). The availability of the precursor, tryptophan, is a glaring variation in melatonin synthesis between animals and plants. Animals must consume tryptophan through diet because they cannot synthesize it on their own, unlike plants (Naz et al. 2023). The main melatonin-producing organelles and concentration centres are found to be animal mitochondria, similar to plants (Reiter 1991). In an isotope tracer investigation, the idea of melatonin produced by plants was initially suggested (Murch et al. 2000). Although there is a great deal of controversy surrounding this, it is believed that the biosynthetic pathway for phytomelatonin in vascular plants is comparable to that in animals (Murch et al. 2000; Tan et al. 2013; Zhao et al. 2019). Axelrod's team first identified the mammalian melatonin biosynthesis route in 1960, and it is now well understood (Hardeland and Poeggeler 2003). The two functional groups of an indoleamine N-acetyl-5-methoxytryptamine (melatonin) have significance for the specificity of receptor binding, as well as for the molecule's amphiphilicity, which allows it to enter any cell, compartment, or bodily fluid, and, intriguingly, for its oxidation chemistry (Hardeland et al. 2006).

Pathways for biosynthesis appear to be the same. Membrane and nuclear receptors, additional chemical interactions, or binding sites mediate these pleiotropic activities. Hepatic P_{450} monooxygenases mostly convert circulating melatonin to 6-hydroxyl and excrete it as 6-sulfatoxymelatonin. The relevance of pyrrole-ring cleavage is of the greater importance in other tissues, notably the brain. Photocatalytic, enzymatic, pseudoenzymatic, and multiple free-radical processes combine to produce the end product, N^1-acetyl-N^2-formyl-5-methoxykynuramine. Hydroxylation and nitrosation lead to the production of additional metabolites. N^1-acetyl-5-methoxykynuramine, a secondary metabolite, promotes mitochondrial activity and suppresses cyclooxygenase-2 (Hardeland et al. 2006).

Tryptophan is assumed as the first substrate of the biosynthesis of melatonin and is engaged in four enzymatic steps that are catalysed by at least six enzymes, according to a number of research: including COMT (caffeic acid-*O*-

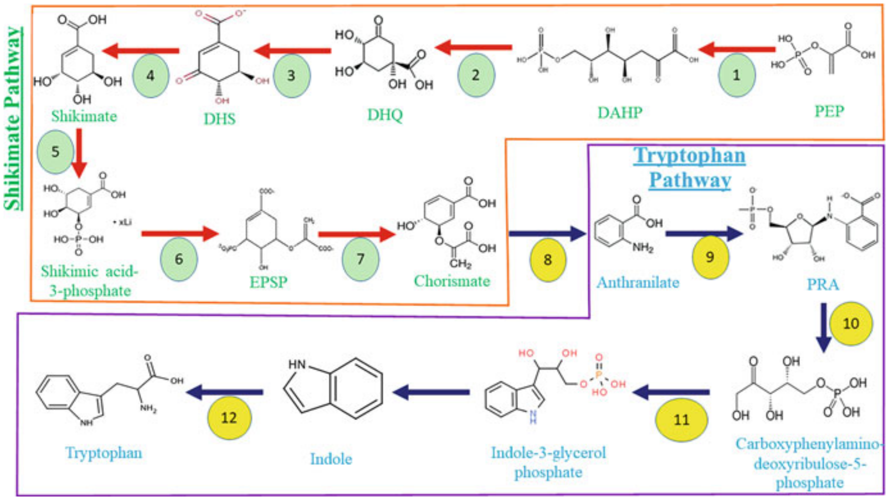

Fig. 1.5 Tryptophan, a major ingredient in the production of melatonin in plants, is produced by a biosynthetic process. (1) DAHP synthase; (2) DHQ synthase; (3) DHQ dehydratase; (4) Shikimate dehydrogenase; (5) Shikimate kinase; (6) EPSP synthase; (7) Chorismate synthase; (8) Anthranilate synthase; (9) PRPP (phosphoribosyl pyrophosphate) transferase; (10) PRAI (PRA isomerase); (11) IGP synthase; (12) Tryptophan synthase. *PEP* 2-phosphoenolpyruvate, *DAHP* 3-deoxy-Darabinoheptulosonate-7phosphate, *DHQ* 3-dehydroquinic acid, *DHS* 3-dehydroshikimate, *EPSP* 5-enolpyruvylshikimate-3-phosphate, *PRA* Phosporibosyl antranilate

methyltransferase), ASMT (*N*-acetylserotonin methyltransferase), SNAT (serotonin-*N*-acetyltransferase), T5H (tryptamine-5-hydroxylase), TPH (tryptophan hydroxylase), and TDC (tryptophan decarboxylase) (Back et al. 2016; Sun et al. 2021). For the synthesis of melatonin, the two reactions that contribute to tryptophan are hydroxylation and decarboxylation. They have been found in plants that are classified as herbivorous (Ahmad et al. 2023). There are four potential pathways for the biosynthesis of auxin, or IAA (indole-3-acetic acid), which is produced naturally in plants, that is, IAM (indole-3-acetamide), TAM (tryptamine), IAOx (indole-3-acetaldoxime), and IPyA (indole-3-pyruvic acid) (Fig. 1.5). There is still a need for more research into the synthesis of auxin from tryptophan in various crops under abiotic stress. N-acetylserotonin is produced by the catalysis of serotonin by SNATs, which is then methoxylated by ASMTs to produce melatonin (Ahmad et al. 2023).

Tryptophan is the precursor of melatonin production and is an amino acid that plants can synthesize de novo through the shikimate pathway. All aromatic amino acids, including tryptophan, can be biosynthesized in plants using this process, which entails seven distinct stages. Briefly,

1. The enzyme DAHP synthase (EC 2.5.1.54) is responsible for converting PEP (phosphoenol pyruvate) and erythrose-4-phosphate into DAHP (3-Deoxy-D-arabinoheptulosonate-7-phosphate). DHQ synthase (EC 4.2.3.4) is an enzyme

that cyclizes DAHP into the 3-dehydroquinate form of DHQ by cyclizing DAHP into DHQ.

2. DHQ dehydratase (EC 4.2.1.10) catalyses the dehydration which converts DHQ (3-dehydroquinic acid) into DHS (3-dehydroshikimate). Shikimate dehydrogenase (EC 1.1.1.25) further catalyses the dehydrogenation reaction, which converts DHS (3-dehydroshikimate) into Shikimate.
3. The enzyme EPSP synthase (EC 2.5.1.19) transforms shikimate into EPSP (5-enolpyruvylshikimate-3-phosphate) after shikimate has been phosphorylated by the enzyme shikimate kinase (EC 2.7.1.71).
4. The enzyme chorismate synthase (EC 4.2.3.5), the crucial stage in tryptophan biosynthesis, which transforms EPSP into chorismate, produces chorismite.
5. Anthranilate synthase (EC 4.1.3.27) converts chorismate into anthranilate, which is then combined with PRPP (phosphoribosyl pyrophosphate) to produce PRA (phosphoribosyl anthranilate).
6. To create indole-3-glycerol phosphate, which is then spontaneously transformed into the indole scaffold, the ribose ring added in this final process is first opened by PRAI (PRA isomerase; EC 5.3.1.24).
7. The final step in the production of tryptophan is the action of TPS (tryptophan synthase; EC 4.2.1.20), which is responsible for the interaction of indole with serine (Mannino et al. 2021).

COMT, ASMT, and SNAT are three different enzymes, each of which may have several isoforms, which are required for two-step processes that produce melatonin from serotonin (Back et al. 2016). While the other two enzymes are methyltransferases, the first enzyme catalyses acetylation. Since serotonin, N-acetylserotonin, and 5-methoxytryptamine are substrates for all three enzymes, the order in which they function can also change in this situation (Park et al. 2013; Byeon et al. 2014; Lee et al. 2014). The conditions of plant growth determine which pathway is used for melatonin production (Fig. 1.6). In fact, the metabolic pathway from tryptophan to melatonin passes through the "tryptamine/serotonin/N-acetylserotonin intermediate" before arriving at melatonin under stressful or normal circumstances that do not create a substantial accumulation of serotonin (Byeon et al. 2015).

The initial step in the biosynthesis of melatonin in plants corresponds to the generation of serotonin from tryptophan. Two distinct routes might be implicated.

(a) In the first route, tryptophan is first decarboxylated by TPH into tryptamine, which TDC subsequently hydroxylates into serotonin.
(b) "TDC converts 5-hydroxytryptophan into serotonin by decarboxylation" follows the "TPH-mediated hydroxylation of tryptophan into 5-hydroxytryptophan, " another alternative.

Both of these approaches are feasible since TDC exhibits strong in vitro affinities for tryptophan and 5-hydroxytryptophan. Decarboxylation has been shown to occur more frequently in plants than hydroxylation as a preliminary step, though (Back

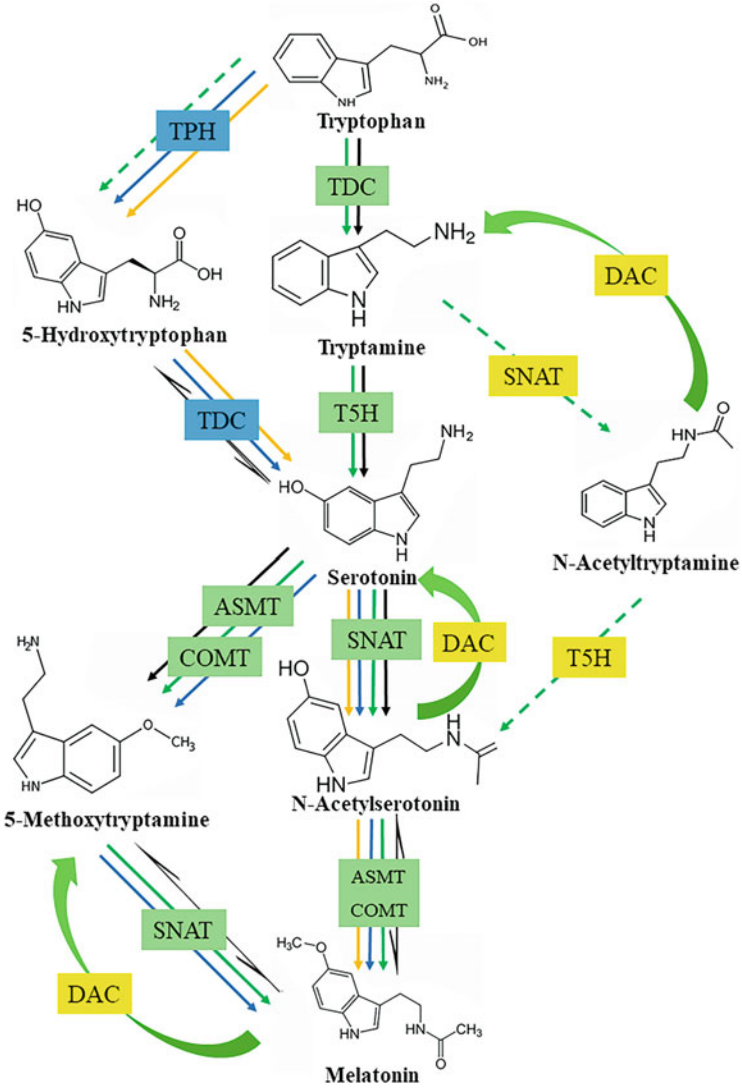

Fig. 1.6 Melatonin biosynthesis mechanisms in microbes, humans, and plants. Green (plants), blue (animals), yellow (bacteria), and black (yeasts) are represented by various arrow colours. Unproven reactions are indicated by dashed lines. *TPH* tryptophan hydroxylase, *TDC* L-tryptophan decarboxylase, *T5H* tryptamine-5-hydroxylase, *SNAT* serotonin *N*-acetyltransferase, *ASMT* acetylserotonin *O*-methyltransferase, *COMT* caffeic acid 3-*O*-methyltransferase, *DAC* deacetylases

et al. 2016). An acetylated substance produced from serotonin is melatonin. The biosynthetic process in which the amino acid tryptophan produces indolic amines has been effectively examined in plants and mammals (Tan et al. 2015; Back et al. 2016).

In plants,

1. The enzyme TDC (tryptophan decarboxylase) transforms tryptophan into tryptamine (Fig. 1.6).
2. The enzyme T5H (tryptamine-5-hydroxylase), which has been widely researched in rice, converts tryptamine into serotonin (5-hydroxytryptamine) but has not been well investigated.
3. SNAT (serotonin *N*-acetyltransferase) is *N*-acetylated serotonin. The hydroxyindole-*O*-methyltransferase i.e., ASMT (acetylserotonin methyltransferase) then methylates *N*-acetylserotonin to produce melatonin. COMT (caffeic acid-*O*-methyltransferase), an enzyme with a broad range of potential substrates, such as quercetin and caffeic acid, can methylate *N*-acetylserotonin in plants, as well (Byeon et al. 2014).
4. After SNAT takes effect, serotonin may also be converted by ASMT/COMT into 5-methoxytryptamine to produce melatonin. In times of stress or senescence, this approach would take place (Back et al. 2016; Tan et al. 2016).

TPH (tryptophan hydroxylase) and TDC (tryptophan decarboxylase) operate in sequence to convert 5-hydroxytryptophan into serotonin in mammalian cells. The occurrence of 5-hydroxytryptophan revealed that certain enzymatic activities, including the action of TPH, operate with a reduced degree in the plant cells even though TPH was not identified in plants. Furthermore, according to several authors, 5-methoxytryptamine can be converted into melatonin under stress, suggesting that plant cells have greater potential for metabolic adaptation than animal cells do. This suggests that the melatonin biosynthesis pathway may take many different kinds of alternative routes (Arnao and Hernández-Ruiz 2014; Tan et al. 2016).

There are five enzymatic stages in the process (Fig. 1.7). Tryptophan is first hydroxylated by TPH to 5-hydroxytryptophan, which is then decarboxylated by the AADC (aromatic amino acid decarboxylase) to serotonin (5-hydroxytryptamine). For many years, the two last phases were ambiguous. In fact, neither the site of melatonin's biosynthesis process nor the specific enzymes required for it were acknowledged to participate in the synthesis. When the mammalian melatonin biosynthetic route was found in 1960, it had been anticipated that only the pineal gland and liver are capable of acetylating serotonin to produce N-acetylserotonin (Pevet et al. 2017). It was incorrectly assumed that melatonin synthesis was not specialized in the liver, because ASMT was the first to be discovered in the pineal gland. Melatonin was first distinguished as a pineal-related neurohormone because of this. The production of melatonin by several organs and tissues in the periphery, including the skin, gut, hepatic cholangiocytes, lymphocytes, bone marrow, testis, ovary, Harderian gland, and retina, is currently well understood (Hardeland et al. 2011).

Because of the enzyme activity of ASMT for *N*-acetylserotonin was found to be around 14 times more potent, it was determined that this compound was the most suitable substrate of ASMT, as compared with the serotonin (Skene 2003). Based on these findings, it was hypothesized that firstly, AANAT acetylates serotonin in order

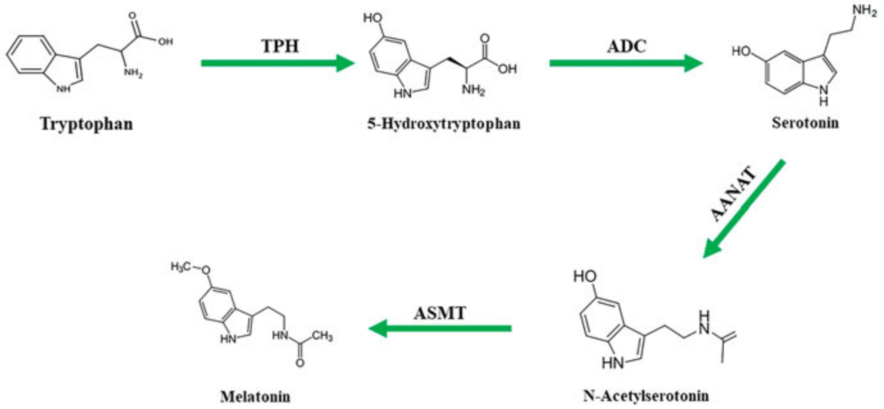

Fig. 1.7 The conventional melatonin synthesis pathway in mammals. TPH Tryptophan hydroxylase, *AADC* aromatic amino acid decarboxylase, AANAT aralkylamine *N*-acetyltransferase, *ASMT* acetylserotonin *O*-methyltransferase

to generate N-acetylserotonin, and that ASMT then converts the subsequent N-acetylserotonin into melatonin. It is generally acknowledged that AANAT is the enzyme that limits melatonin synthesis, i.e., a limiting factor. In fact, blue light (420–480 nm) is the primary regulating component in the melatonin synthesis process in animals (Ganguly et al. 2005). This type of daytime irradiation reduces the production of melatonin instantaneously by impairing AANAT's ability to function both through protein dephosphorylation and downregulation of gene expression (Tan et al. 2011; Venegas et al. 2012). Other variables that could interfere with an animal's ability to produce melatonin include fluctuations in temperature, food consumption, and various kinds of health conditions (Mannino et al. 2021). N-acetyltryptamine, which is produced by SNAT, may be transformed by T5H into N-acetylserotonin, which is subsequently manufactured as melatonin (Arnao et al. 2023).

1.5 Conclusion/Future Directions

Several recent studies have established the critical significance of melatonin in plant processes, notably its control of crop development and productivity. However, a full knowledge of melatonin, which affects crop development and production under abiotic stress conditions, is still inadequate. Other melatonin biosynthetic pathways, including ones independent of serotonin synthesis, may exist. The enzymes involved have yet to be discovered, and those that are known do not appear to be participating in this process. Aromatic and therapeutic plants have greater phytomelatonin levels than conventional veggies. Such botanical medicinal plants are perfect choices for future melatonin supplements. Controlling growing conditions might aid in the production of phytomelatonin-rich plants. Additional investigation on other species and varieties is required. The existence of phytomelatonin in all plant species studied so far suggests that it might be used as a nutraceutical ingredient. The discovery and research of phytomelatonin-rich species and variants should be prioritized. In terms of melatonin intake, we should focus on alternatives to synthetic melatonin and boost organically generated melatonin.

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Melatonin Detection and Quantification Techniques

2

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Abstract

An indolic substance made from tryptophan is called melatonin (N-acetyl-5-methoxytryptamine). This substance, typically classified as a receptor or mammalian hormone, was first found in plants in 1995. Research into plant-based melatonin is an area that is expanding rapidly. Different plants contain different versions of the enzymes involved in the biosynthesis of melatonin. In the twentieth century it was discovered that several plant species can produce this molecule in large quantities and store it in specialized organs. According to endosymbiotic theory, the locations for melatonin biosynthesis in plants are chloroplasts and mitochondria. As plants similar metabolites with mammals, the metabolism of the sleep-inducing hormone melatonin in plants is less well understood. Although our understanding of the melatonin-producing enzymes in plants is still in its infancy, it has been found that plant cells are expected to be more flexible than animal cells. This chapter summarizes about melatonin discovery, evolution, and biosynthesis.

Keywords

Biosynthesis · Evolution · Melatonin · Tryptophan

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2.1 Introduction

Melatonin is a substance with a wide range of uses, especially in both animals and plants. The hormone indoleamine affects a variety of bodily processes, including emotions, slumber, body temperature, the retina, and sexual behaviour. The majority of these factors are controlled by or in combination with the animal's circadian schedule (Fuller et al. 2006; Jan et al. 2009; Altaf et al. 2022). It was discovered in the twentieth century that several plant species may make this molecule in large quantities and store in specific tissues. Melatonin (N-acetyl-5-methoxytryptamine) was first discovered in the bovine pineal gland by the dermatologist Lerner et al. (1958a, b). The term was first connected to its capacity to bind melanin, a pigment granule found in the chromatophores of fish and frog epidermis. Since indolamine functions as a neurohormone in the pineal gland of mammals, it was long believed that melatonin was only made there. However, it is now known that melatonin is also generated by several organisms from the Eukarya and Bacteria domains (Mannino et al. 2021a, b). It is a multifunctional signalling molecule that is widely distributed throughout a plant's many organs and is in charge of inducing a number of physiochemical reactions in response to harmful environmental circumstances in different plant systems. It functions as an essential antioxidant in animals and influences a variety of cellular processes, including circadian rhythms, body temperature, sleep, and the immune system (Pieri et al. 1994; Rodriguez et al. 1994; Jan et al. 2009). Melatonin is also an antioxidant agent that may regulate plants' reactive oxygen and nitrogen species. It also functions as an indoleamine neurotransmitter. As a signalling agent, melatonin causes several distinct physiological reactions in plants that may help improve photosynthesis, growth, carbon fixation, root growth, seed germination, and defence against various biotic and abiotic stresses (Van Tassel et al. 2001; Arnao and Hernández-Ruiz 2015; Sun et al. 2015; Wei et al. 2018; Zhang et al. 2018; Altaf et al. 2021; Arnao and Hernández-Ruiz 2019. Melatonin is also known to enhance physiological functions, such as spreading a plant's regular development and protecting emerging tissues from damage and stress signals from the environment (Erland et al. 2015; Altaf et al. 2023). This chapter explores melatonin discovery and divergent biosynthetic pathways in plants more broadly.

2.2 Discovery and Evolution of Melatonin

Melatonin is widely distributed, notably among the earliest bacteria (cyanobacteria and -proteobacteria), suggesting that it is an old molecule that has persisted throughout the history of all creatures (Manchester et al. 2015; Pshenichnyuk et al. 2017). Melatonin may have originated in bacteria before the endosymbiotic relationship, according to a popular theory. Early prokaryotes eventually developed from cyanobacteria and proteobacteria into chloroplasts and mitochondria, respectively. As a result, all unicellular and multicellular organisms eventually manufacture this essential indoleamine in these organelles (Margulis 1975; Tan et al. 2013; Behera et al. 2022; Reiter et al. 2017a, b). Melatonin is universally expanded to all creatures with species diversity, and as a result, its functions, synthesis route, production locations, and biosynthetic control have also varied. Melatonin's detoxification of free radicals produced by photosynthesis and metabolism was thought to be its primary intent (Manchester et al. 2015; Tan et al. 1993, 2010, 2015; Galano et al. 2018). Melatonin evolved into a pleiotropic molecule with biodiversification during organismal evolution, which affects biological rhythms, reduces inflammation, etc. Melatonin also resists oxidation-related stress (Tan et al. 2010; Lochner et al. 2018; Chourasia et al. 2021; Onaolapo and Onaolapo 2018; Tamtaji et al. 2018). Organisms have created a variety of systems to control the manufacture of melatonin in order to benefit from its many biological effects. For instance, the transcription factor activator protein-1 (AP-1) stimulates the genes involved in melatonin synthesis while under stress to increase the production of melatonin (Rodriguez et al. 1994; Estrada-Rodgers et al. 1998; Korkmaz et al. 2009; Muxel et al. 2016; Cai et al. 2017).

Around 2.5 billion years ago, the Earth's atmosphere saw a surge in molecular oxygen (O_2) as a result of the persistent release of this gas by photosynthetic microorganisms that had originated about a billion years earlier (the Great Oxygenation Event). The increase in atmospheric oxygen exerted a huge selection pressure on species to evolve O_2 metabolism (Kump and Barley 2007; Reiter et al. 2017a, b; Chourasia et al. 2022). Reactive oxygen species (ROS) are inevitably produced during aerobic metabolism when oxygen takes leaky electrons from the electron transport chain (ETC).

According to estimates, up to 4% of the oxygen that organisms use throughout their aerobic metabolism is eventually converted to ROS (Casteilla et al. 2001; Treberg et al. 2018). Since these high levels of ROS are hazardous to cells and organisms, elaborate and efficient methods to counteract them have been developed; this first happened in early life forms like bacteria and later unicellular creatures (Case 2017). Melatonin likely first appeared in early photosynthetic prokaryotic bacteria as an antioxidant and free radical scavenger to combat oxidative stress (Tan et al. 2013; Devi et al. 2022; Reiter et al. 2017a, b). In all living things, melatonin has maintained its capacity to reduce oxidative stress, which is brought on by the generation of free radicals during photosynthesis and respiration (Manchester et al. 2015). Based on its capacity to donate an electron or a hydrogen atom, or depending on the kind of radical, may be by other mechanisms as well, the unique structure of melatonin dictates its high efficacy in detoxifying free radicals (Shi et al. 2016). The cascade reaction, which takes place when melatonin produces derivatives that are also free radical scavengers, is at least largely responsible for its higher antioxidant potential to reduce oxidative stress (Tan et al. 2013). The molecular makeup of melatonin has not altered in billions of years, despite its extremely extensive evolutionary history and numerous roles (Reiter et al. 2017a, b). Furthermore, despite all creatures' extremely high levels of biodiversification during evolution, melatonin may have been kept by all of them. This pertains to the fact that mitochondria and chloroplasts (or both) are conserved in the majority of species' cells. Red blood cells are one exception, since they expel various organelles, including mitochondria, during erythropoiesis. Cyclic 3-hydroxymelatonin and other melatonin metabolites are produced when melatonin interacts with different ROS. These metabolites serve as radical scavengers, sometimes even more aggressively than melatonin in their ability to neutralize ROS (Lee et al. 2016; Kumar et al. 2023a, b).

Melatonin has been shown to play a variety of roles in the growth and development of plants, including seed protection and germination, root development, fruit ripening, and senescence (Liang et al. 2017; Kumar et al. 2022b). Due to their sessile nature, plants experience more environmental challenges than mammals do. They quickly upregulate the production of melatonin as a defence against these pressures, which helps them avoid the oxidative damage that thes. In animals, quinone reductase 2 (QR2, E.C. 1.10.99.2), a cytosolic molecule, also binds directly to the catalytic site to influence the activity of this enzyme; this modulation may be either up- or downregulation (Boutin et al. 2008). Importantly, the modification in QR2 activity might also be crucial for the production or detoxification of ROS (Reybier et al. 2011).

2.3 Origin of Melatonin Receptors

The only thing the cell needed to do for melatonin to fulfil its putative original purpose, i.e., act as a direct free radical scavenger, was to place it close to where the majority of ROS are often produced. An antioxidant must be positioned in this way because free radicals have a very short half-life and instantly destroy molecules in the area around where they are generated. The initial harm caused by a highly reactive radical cannot be stopped if a free radical scavenger is not placed correctly. Evolution designed the uptake and production of melatonin in chloroplasts (Choi et al. 2017) and mitochondria (Suofu et al. 2017; Kumar et al. 2023b; Acuna-Castroviejo et al. 2018)—both significant sources of the overall oxidative burden of cells—to achieve this correct placement. Melatonin has an exceptionally wide range of physiological tools in vertebrates that are still alive today. It was essential for its binding sites/receptors and related signalling transduction mechanisms to evolve in order to increase its range of functional possibilities. The outer membrane of mitochondria has recently been linked to the MT1 receptor, which is typically thought to be restricted to the limiting membrane of cells. They developed the word "automitocrine" to describe this mechanism. According to the researchers who made this discovery, melatonin diffuses out of these structures and interacts with MT1 receptors on the outer membrane of these organelles. Melatonin produced by mitochondria may regulate the release of cytochrome c from the matrix through this receptor-mediated mechanism. This self-regulatory mechanism affects apoptosis that results from significant free radical damage. There are binding sites in the cytosol (Boutin and Ferry 2019) and the nucleus in addition to the well-studied and highly relevant cell membrane receptors that are essential for a number of melatonin's key functions (Hill et al. 2009; Wang et al. 2015; Zhao et al. 2017). Quinone reductase 2 (QR2) has been classified as receptor MT3 in the cytosol (Boutin 2016; Kumar et al. 2022a). Some of the ways that melatonin reduces oxidative damage may be connected to the activity of this detoxifying enzyme. Additionally, melatonin interacts with calmodulin in the cytosol, which is thought to be related to the indoleamine's stated ability to prevent cancer growth (Menendez-Menendez and Martinez-Campa 2018).

Land plants have many of the antioxidant enzymes found in mammals, in addition to melatonin's direct scavenging of radicals and their byproducts. When exposed to an abiotic stress, such as a draught, heat, cold, toxin, etc., plants' melatonin-influenced enzymes are rapidly upregulated (Arnao and Hernández-Ruiz 2015; Shi et al. 2015). Melatonin receptors are thought to be involved in this upregulation, as is probably the case for mammals as well.

2.4 Melatonin Biosynthesis in Plants and Animals

Melatonin probably developed in bacteria; it has been detected in both photosynthetic cyanobacteria and in a-proteobacteria. For the first time, Lerner and colleagues reported the existence of melatonin in the bovine pineal gland in 1958 (Lerner et al. 1958a, b). After being isolated and discovered in the cow's pineal gland, melatonin was later discovered in a variety of other plants and animals (Lerner et al. 1958a, b; Kumar et al. 2023a, b; Hattori et al. 1995). Melatonin is widely distributed, particularly in cyanobacteria and a-proteobacteria, which suggests that it is an ancestral molecule that has persisted throughout the evolution of all organisms (Manchester et al. 2015) (Fig. 2.1). Its original association with the name was its capacity to bind pigment granules (melanin) in the chromatophores of fish and frog epidermis. Since indolamine functions as a neurohormone in the pineal gland of animals, it was believed for more than 30 years that melatonin was only produced there. However, it is now known that melatonin is also produced by several organisms in the Eukarya and Bacteria domains, while no information has been found for Archaea. N-acetyl-5-methoxytryptamine, also known as melatonin, was first found in 1959 (Lerner et al. 1959). Soon after, the biosynthetic route from tryptophan, using serotonin as an intermediary, was revealed (Lauber et al. 1968). Melatonin was first discovered in humans in 1959, and in the 1960s and 1970s, numerous animals and vertebrates, including birds, frogs, and fish, were found to contain it (Baker et al. 1965; Axelrod and Weissbach 1960). All living things, including microbes, yeast, fungus, animals, and plants, are believed to synthesize melatonin (Reiter et al. 2013). According to research, plants' mitochondria and chloroplasts have the greatest amounts of melatonin of any cellular compartment (Kanwar et al. 2018). This finding, along with evidence that serotonin N-acetyltransferase (SNAT), one of the rate-limiting enzymes involved in melatonin production, is localized in mitochondria and chloroplasts, points to the hypothesis that these cells are the primary locations for this indolamine's biosynthesis (Yu et al. 2019; Wang et al. 2017). Tryptophan serves as the only amino acid that goes into building this molecule. Although tryptophan is a dietary component, some species can also make it using the shikimic acid route, which begins with D-erythrose-4-phosphate, phosphoenolpyruvate, or carbon dioxide (Bochkov et al. 2012). The only amino acid used to make this protein is

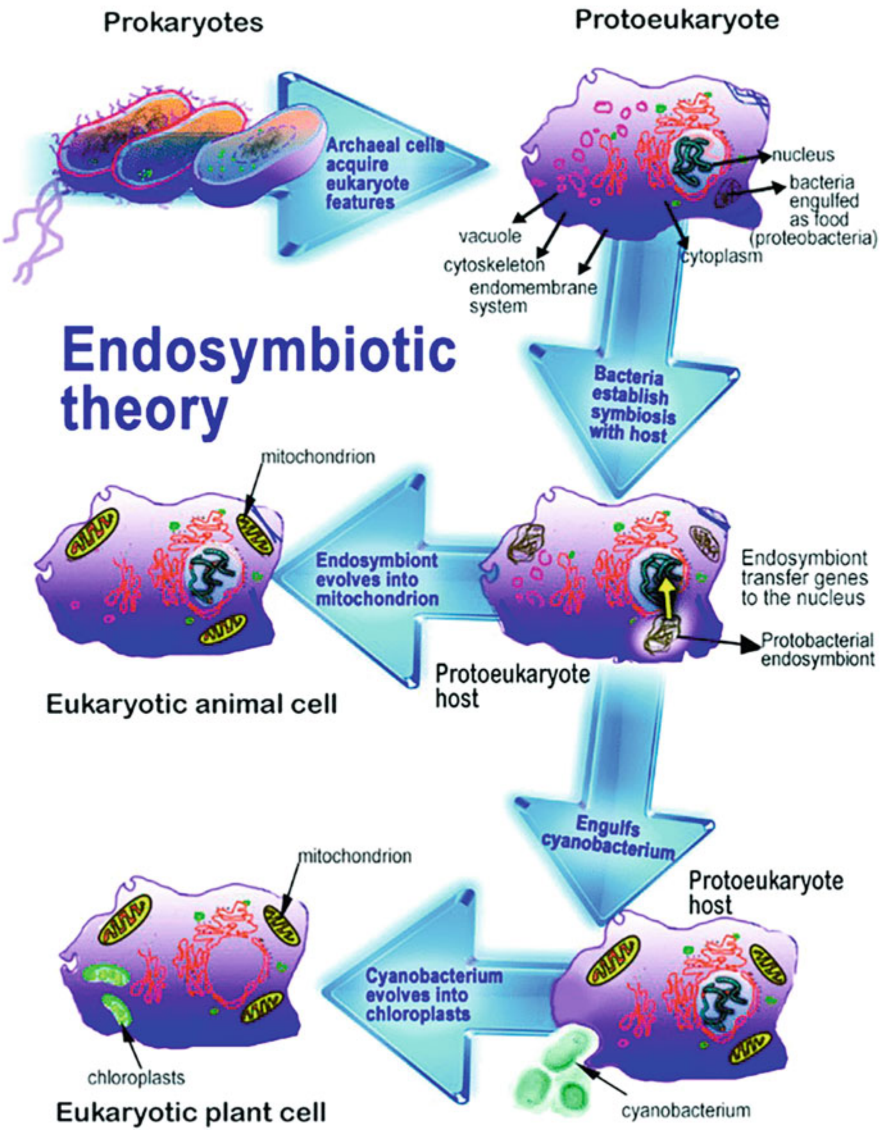

Fig. 2.1 This figure illustrates the endosymbiotic origin of mitochondria and chloroplasts. a-Proteobacteria (Source: Zhao et al. 2019)

tryptophan. Although tryptophan is a dietary component, some species also have the ability to synthesize it using the shikimic acid route, which begins with Derythrose-4-phosphate, phosphoenolpyruvate, or carbon dioxide (Bochkov et al. 2012; Lal et al. 2021b). Bacteria, fungi, and plants maintained the capacity to synthesize tryptophan with the evolution of organisms (apart from animals). Conversely, animals can only get the essential amino acid tryptophan through eating. When tryptophan levels are lower than they are in plants, mammals produce significantly less melatonin than do plants. Since plants are unable to behaviourally prevent highly stressful situations, they need additional stress protection. In order to ensure that melatonin is available to reduce oxidative stress levels under stressful environmental circumstances, tryptophan biosynthesis is likely maintained in plants. Serotonin is first produced by decarboxylation and hydroxylation of tryptophan. There are two methods for serotonin synthesis that result in the production of melatonin in various taxa. Microorganisms and plants have a distinct serotonin biosynthetic pathway than mammals do. In plants, tryptophan is converted to tryptamine by the enzyme tryptophan decarboxylase (TDC), which is followed by the enzyme tryptamine 5-hydroxylase (T5H), which catalyses the serotonin biosynthesis (Park et al. 2008). However, animals first hydroxylate tryptophan using tryptophan hydroxylase (TPH) to form 5-hydroxytryptophan, which is then decarboxylated by aromatic amino acid decarboxylase (AADC) to produce serotonin. This is in contrast to humans, who first produce tryptophan through the decarboxylation of the amino acid. Serotonin is a crucial intermediate between tryptophan and melatonin, following which the biosynthetic process uses two potential pathways, each of which involves two consecutive enzymatic processes that produce melatonin (Back et al. 2016). These processes use the enzymes serotonin N-acetyltransferase (NAT) and acetylserotonin O-methyltransferase (ASMT; formerly known as hydroxyindole-O-methyltransferase, HIOMT) to catalyse the conversion of serotonin into the end product, melatonin. While the final enzyme, ASMT, catalyses NAS to produce melatonin, the penultimate enzyme, NAT, plays a critical part in the conversion of serotonin to N-acetylserotonin (Byeon et al. 2016).

Tryptophan and the other aromatic amino acids can be biosynthesized in plants through this pathway, which comprises seven distinct stages (Mannino et al. 2021a, b) as shown in Fig. 2.2.

In all species, melatonin production involves four enzymatic stages starting with tryptophan. The melatonin production rhythm evolved over billions of years, becoming more diverse. There are two stages in the production of melatonin from tryptophan (Fig. 2.3). Serotonin is produced from tryptophan in the first stage of the melatonin biosynthesis pathway in plants.

2.5 Melatonin Detection and Quantification

Melatonin (N-acetyl-5-methoxy-tryptamine) was initially discovered in 1958 and it was given that name because it could counteract the melanocyte stimulating hormone (MSH)-induced darkening. It is a ubiquitous chemical found in both plants and mammals. It has been found at various levels in many types of plants and organs.

Melatonin operates as a hormone similar to indole-3-acetic acid because it has the same starting biosynthesis component with auxin in plants (Fig. 2.4). In lupin hypocotyls, as well as in monocot species like canary grass, wheat, barley, and oat (Hernández-Ruiz et al. 2005; Lal et al. 2022b; Arnao and Hernández-Ruiz 2007),

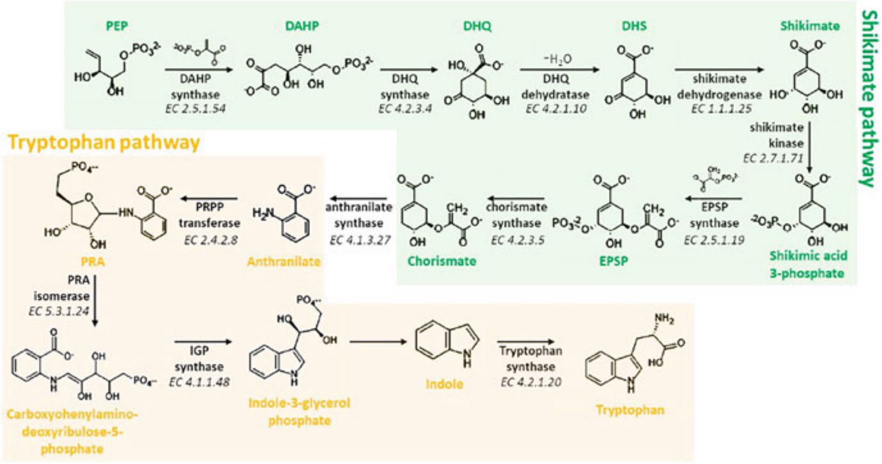

Fig. 2.2 Biosynthetic pathway involved in the synthesis of tryptophan, the key compound of melatonin in plants. *DAHP* 3-Deoxy-D-arabino-heptulosonate 7-phosphate, *DHQ* 3-Dehydroquinate, *DHS* 3-Dehydroshikimate, *EPSP* 5-Enolpyruvylshikimate 3-phosphate; IGP synthase, Indole-3-glycerol phosphate synthase, *PEP* phosphoenolpyruvate, *PRA* Phosphoribosyl anthranilate, *PRPP* 5-Phospho-ribosyl 1-pyrophosphate

and dicot species like Arabidopsis, melatonin is thought to be a growth-promoting chemical, similar to auxin. As such, it is an auxinic hormone in plants. By directly scavenging reactive oxygen species and through indirect mechanisms that boost antioxidative enzyme activity, photosynthetic efficiency, and metabolite content, melatonin increases plants' ability to withstand stress. It also plays an important role in regulating gene expression.

A plant's melatonin production is thought to be for its own defence against free radicals produced by environmental or metabolic activities, such as photosynthesis (Manchester et al. 2000). To corroborate this, it has been shown that the sensitivity of *Nicotiana tabacum* leaves to ozone (a free radical producer) damage varies among kinds, with the susceptibility decreasing in leaves with the greatest melatonin contents (Dubbels et al. 1995). This is in line with the theory that melatonin serves as an antioxidant in both plants and mammals. The seeds of edible plants have also been shown to contain significant quantities of melatonin (Manchester et al. 2000). Melatonin is thought to be crucial for seeds' ability to protect germ and reproductive organs from oxidative damage brought on by UV radiation, drought, extremely high or low temperatures, and other environmental factors.

To gain deeper understanding of melatonin's involvement in plant physiology and ecology, it is fundamental to establish more dependable analytical methods for melatonin detection and quantification. For materials ranging from algae to higher plants, melatonin was extracted, purified, and measured using a variety of techniques. Simple extraction solvents such ethanol, 10% Na2CO3, phosphate-buffered saline, or potassium phosphate buffer were employed by several writers (Dubbels et al. 1995; Hattori et al. 1995; Lal et al. 2021a; Manchester et al. 2000).

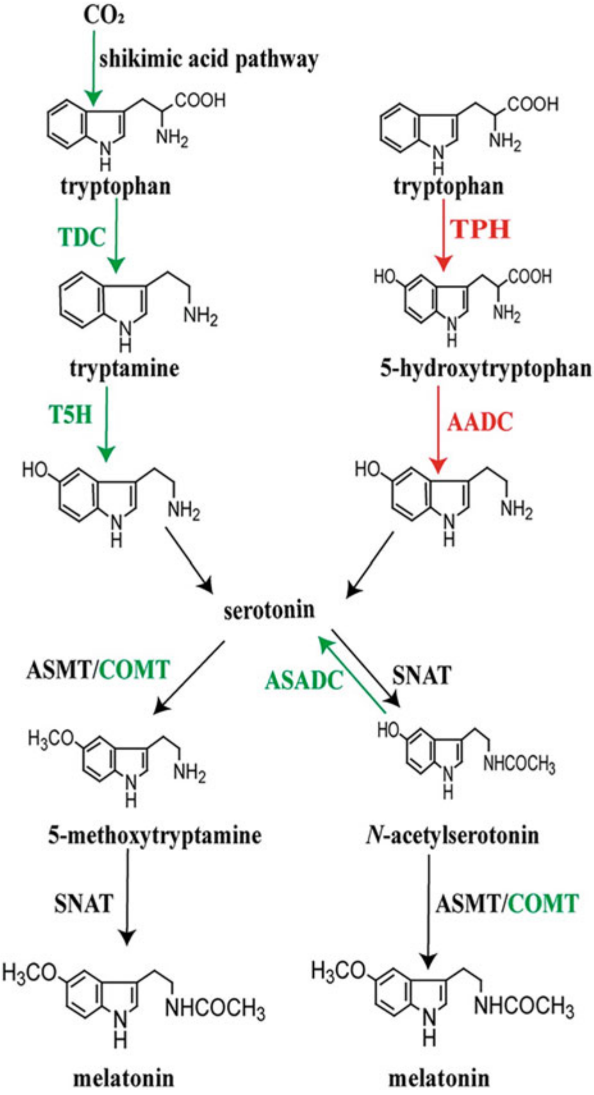

Fig. 2.3 Pathways of melatonin synthesis in different plant (left) and animal (right) sources; (Zhao et al. 2019). *AADC* aromatic L-amino acid decarboxylase, *ASMT* acetylserotonin O-methyltransferase, *COMT* catechol-O-methyltransferase, *SNAT* serotonin N-acetyltransferase, *T5H* tryptamine 5-hydroxylase, *TPH* tryptophan hydroxylase

Poeggeler and Hardeland (1994) drew attention to the fact that material from unicellular eukaryotes and plants frequently includes substances (for instance, chelated iron or redox-active proteins) that encourage melatonin breakdown by photo-oxidation or free radical-mediated oxidation. Methods that had been used to measure melatonin in animals were applied to plants. The sensitivity and specificity of the approaches vary. Although HPLC with fluorescence detection was successfully utilized to measure melatonin in Chinese medicinal herbs, it was not sensitive enough to demonstrate its presence in *C. rubrum* shoots (Chen et al. 2003). Melatonin has recently been identified subjectively and quantitatively in edible plants and

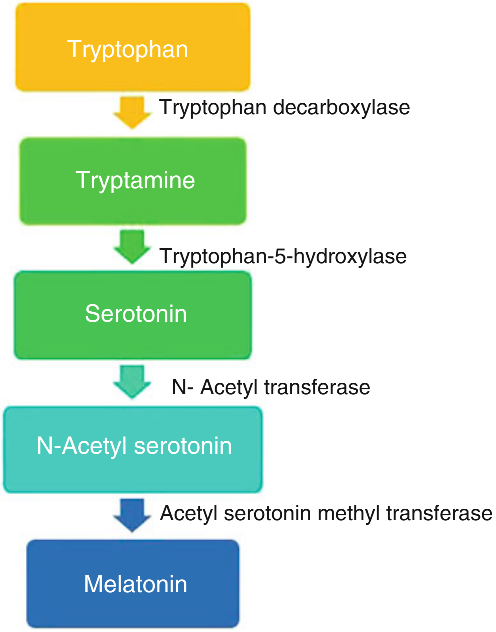

Fig. 2.4 Biosynthesis of melatonin

animal diets. Many fruits and vegetables contain melatonin, according to researchers such as blackberry, black mulberry, white mulberry, radish, jujube, clove, and sweet cherry (Riga et al. 2014; González-Gómez et al. 2009). Analytical methods are required for the quick and precise measurement and quantification of melatonin in soporific medications due to the numerous favourable benefits of melatonin on human health, most notably its intense usage in avoiding sleeplessness. Numerous techniques have been published for measuring melatonin in various types of matrix, such as plasma, saliva, pineal gland, and biological materials using GC-MS chemical ionization (Fourtillan et al. 1994), HPLC chemiluminescence (Lu et al. 2002), HPLC-FLD (Rizzo et al. 2002), LC-MS/MS (Eriksson et al. 2003), and HPLC-electrochemical detector (Chanut et al. 1998). There are many more approaches for quantifying melatonin such as electrochemical, bioanalytical, and analytical (Stege et al. 2010; Lal et al. 2022a; Radi and Bekhiet 1998). None of the methods employs ambient mass spectrometry, although it would provide a cheap and fast alternative to conventional methods (Black et al. 2016). Out of them, the liquid chromatography approach has been frequently utilized. In contrast, HPLC with electrochemical detection is more sensitive and was often utilized in algae and higher plants. Despite having a very low specificity, melatonin may have retention periods that are extremely similar to those of other substances with comparable oxidation potential. Melatonin levels in plants measured solely by RIA and not verified by other techniques may therefore be exaggerated, as was shown, for instance, for Pharbitis nil and tomato. Melatonin RIA is therefore not a valid approach in plants as opposed to mammals. The issues raised above can be resolved by using gas chromatography-mass spectrometry (GC-MS) or low-cost mass spectrometry (LC-MS), which provide high sensitivity and great detection specificity (Dubbels et al. 1995; Van Tassel et al. 2001). Another one, AnFD has low limits of detection and quantification, is adaptable and sensitive enough to quantify melatonin in samples with low melatonin levels (Milenkovic-Andjelkovic et al. 2015; Setyaningsih et al. 2015). The extraction of melatonin can be greatly impacted by a variety of factors, including the extraction solvent and extraction time. The polarity and diffusivity of the solvent used determine how well target chemicals are extracted from plant samples. Depending on the polar characteristics of the substance to be extracted, the polarity of the solvent influences the extraction (Setyaningsih et al. 2015).

2.6 Quantification

A method where representable units are selected from a large sample is quantification. A number of plant-derived chemicals may interact with related antibodies and enzymes, leading to an overestimation of the true levels of melatonin.

2.6.1 Chromatographical Procedures

Chromatographic approach is the most used separation method for melatonin. The process of separating, purifying, and analysing chemicals is known as chromatography. The word "chromatography" comes from the Greek words "chroma" and "graphein," which in turn mean "to write".

2.6.2 Brief Procedure of Chromatography

The mixture to be separated is applied to a stationary phase (solid or liquid) in this procedure, and a pure solvent—such as water or any gas—is then allowed to move slowly across the stationary phase, transferring the components separately according to their solubility in the pure solvent.

Advantage of GC-MS is that it provides great sensitivity and specificity, and the drawback is the requirement for derivation. HPLC techniques are more effective and precise, and they do not need to be derivatized. For melatonin separation, the majority of HPLC techniques have utilized reverse-phase columns (RP C18 or RP C8), and two distinct detectors, ECD and FD, have been utilized in fruits (Table 2.1). By using HPLCeECD (Table 2.1) and acetonitrile in an 80:20 ratio with 0.1 M potassium phosphate buffer (pH 14 4.5) at a flow rate of 1 mL/min, the presence of melatonin in tart cherries was determined. Garcia-Parrilla et al. (2009) found that HPLCeFD was sensitive and versatile in its capacity to measure melatonin in fruits and had a low limit of detection and quantification. MV-Rainin instead of Zorbax was proved to be more selective towards matrix compounds present in the grappa (Mercolini et al. 2012). The mobile phase typically comprised of acetonitrile and

Table 2.1 Methods that have been adopted in various crops for melatonin extraction

Crops	Extraction solvent	Analytical method
Hordeum vulgare	Chloroform	LC-FLD
Lupinus spp.	Chloroform	LC-FLD
Oryza sativa	Methanol	LC-FLD
	Methanol	LC-MS
Datura metel (seed and flower)	80% methanol	LC-MS
Helianthus annus L.	1 M Tris-HCl, 0.4 M perchloric acid, 0.1%EDTA, 0.05% Na2S2O5, 10 M ascorbic acid	LC-UV
Arabidopsis thaliana	50% methanol	LC-MS
Cynodon dactylon	89% acetone, 10% methanol	ELISA
Musa sp.	10%Na_2CO_3 and diethyl ether	RIA and GC-MS
Malus pumila, *Ananas comosus*	10 mm PBS buffer	RIA
Ananas comosus, *Mangifera indica*	Methanol and C18 cartridges	HPLC-FD and ELISA
Musa sp., *Ananas comosus, Punica granatum*	10%Na_2CO_3 and diethyl ether	GC-MS
Vitis Vinifera	Methanol and C18 cartridges	HPLC-FD and ELISA
Vitis Vinifera	5 g/L tartaric acid in water/ethanol mixture and C8 sorbent	HPLC-FD
Prunus avium	50 mm Pbs buffer and chloroform	HPLC-MS
Fragaria ananassa	Acetone and C18 cartridges	HPLC-MS
Montmorency, Balaton tart cherry	Methanol and C18 cartridges	HPLC-MS
Montmorency, Balaton tart cherry	50 mm K_3PO_4 buffer and chloroform	HPLC-ECD

LC-FLD liquid chromatography with fluorescence detection, *LC-MS* liquid chromatography-mass spectrometry, *LC-UV* liquid chromatography with ultraviolet detection, *ELISA* enzyme-linked immunosorbent assay, *RIA* radioimmunoassay, *GC-MS* gas chromatography-mass spectrometry, *HPLC-FD* high-performance liquid chromatography with fluorescence detection, *HPLC-ECD* high-performance liquid chromatography with electrochemical detection

water in varying ratios. To reduce the retention period, it is preferable to raise the concentration of organic solvents in the mobile phase because there is no upper limit for their concentration in HPLCeFD (Huang and Mazza 2011). Consequently, compared to HPLCeECD, HPLCeFD provides a superior potential for melatonin detection.

2.6.3 Extraction of Melatonin

For purification and to prevent clogging of the HPLC column, C18 solid phase extraction (SPE) can be combined with acetone and PCA extraction techniques. Many medicinal plants were found to have substantially greater melatonin concentrations, as shown by experiments using SPE and HPLC (Chen et al. 2003). The intrinsic selectivity of this HPLC application is enhanced by combining melatonin derivatization with HPLC purification to produce a product with a distinct fluorescence spectrum and retention time under the same chromatographic conditions. For the first time, this technique was utilized to quantify melatonin in photoautotrophic organisms. It involves the conversion of melatonin to 6-MOQMA (Iinuma et al. 1999).

Liquid extraction using 10% Na_2CO_3 and diethyl ether was used to extract melatonin from bananas. RIA (radioimmunoassay) kits were also used in cabbage, spinach, radish, etc. (Dubbels et al. 1995). Melatonin was extracted from apples, pineapples, strawberries, and pomegranates using a similar sequential process (Badria 2002). Using phosphate buffer and chloroform, melatonin in cherries was extracted, and the recovery rates from sour and sweet cherries, respectively, were 60% and 70.7% (Burkhardt et al. 2001; González-Gómez et al. 2009).

Melatonin was isolated from grape skins, strawberries, and mangoes using SPE with C18 cartridges (Iriti et al. 2006; Sturtz et al. 2011; Johns et al. 2013). Melatonin may be absorbed by SPE, and its expensive extraction is a significant drawback. According to a different research, the sample pretreatment process known as microextraction by packed sorbent (MEPS) is quicker and less expensive than standard SPE. It also needs less sample and solvent volume for melatonin extraction (Mercolini et al. 2012). It revealed that all examined samples had melatonin recovery rates with MEPS pretreatment that above 90%. Microwave-assisted extraction (MAE) was developed by Setyaningsih et al. (2012) for very accurate melatonin extraction from rice. Because of the novel extraction technique used, they claimed that the average quantity of melatonin in short grain varieties (54.17 13.48 ng/g) is significantly greater than the fig. (1.0 0.06 ng/g) reported by Hattori et al. (1995).

According to Stege et al. (2010), sonication can cause cavitations, which produce microenvironments with high temperatures and high pressures and speed up the removal of analytes from complicated matrices. So, melatonin extraction may also be done with the use of ultrasonography.The whole extraction time can take anywhere between 15 min and more than 16 h, and in most situations, the reader is left to infer the total extraction time based on the length of time for separate procedures like shaking, sonication, or drying.

Light is a major factor that contributes to the degradation of melatonin. Since sonication generates heat even when done in an ice bath, the study conducted by Maharaj and Dukie (2002), found that heat and to a lesser extent sonication had the greatest impact on the stability of melatonin, indicating the importance of temperature on melatonin stability.

2.7 Conclusion

Melatonin functions as a circadian regulator, cytoprotector, and growth promoter in plants, where it has been documented to be engaged in a number of physiological processes. The information presented in this study explains the melatonin's chemical properties as well as the usual biosynthetic routes used by both plants and animals. Melatonin, which is thought to have initially developed to offer molecular defence against free radicals, has acquired additional functions over a very long evolutionary period. Melatonin is thought to have first evolved in microorganisms about 3.0–2.5 billion years ago. Rhizogenesis, cellular growth, and stress defence are additional functions of this compound. In this regard, a number of evaluations with condensed data can be examined. Moreover, the main biochemical and biomolecular differences were highlighted. In fact, the benefits found in previous studies and the lack of toxicity at large doses support the use of this indolamine as a dietary additive for animals and plants. A plant's melatonin production is thought to be for its own defence against free radicals produced by environmental or metabolic activities, such as photosynthesis. To corroborate this, it has been shown that the sensitivity of *Nicotiana tabacum* leaves to ozone (a free radical producer) damage varies among kinds, with the susceptibility decreasing in leaves with the greatest melatonin contents. This is in line with the theory that melatonin serves as an antioxidant in both plants and mammals. Melatonin in significant concentrations has also been found in seeds of edible plants. Hence, melatonin in seeds has been found to be crucial for shielding germ and reproductive organs from oxidative damage brought on by UV radiation, drought, temperature fluctuations, and environmental pollutants.

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3

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

Muhammad Yaseen and Farhan Khalid

Abstract

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

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

Keywords

Melatonin · Germination · Seedling establishment · Development

3.1 Introduction

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

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

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

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

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

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

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

3.2 Melatonin Synthesis and Signaling Pathways in Plants

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

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

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

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

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

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

3.2.1 Biosynthesis of Melatonin in Plants

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

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

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

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

3.2.2 Melatonin Signaling Pathways

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

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

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

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

3.2.3 Interaction of Melatonin with Other Plant Hormones

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

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

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

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

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

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

3.3 Melatonin and Seed Germination

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

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

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

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

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

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

3.3.1 Relationship Between Melatonin on Seed Germination

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

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

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

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

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

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

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

3.3.2 Mechanisms of Melatonin-Mediated Seed Germination

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

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

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

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

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

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

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

3.3.3 Impact of Melatonin on Seedling Growth

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

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

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

3.4 Melatonin and Plant Establishment

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

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

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

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

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

3.4.1 Role of Melatonin in Root Development

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

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

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

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

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

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

3.4.2 Influence of Melatonin on Shoot Growth

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

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

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

3.4.3 Effect of Melatonin on Stress Tolerance During Plant Establishment

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

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

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

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

3.5 Melatonin and Vegetative Development

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

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

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

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

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

3.5.1 Regulation of Melatonin in Vegetative Growth

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

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

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

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

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

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

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

3.5.2 Interaction of Melatonin with Other Plant Hormones During Vegetative Development

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

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

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

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

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

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

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

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

3.5.3 Effect of Melatonin on Plant Architecture

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

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

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

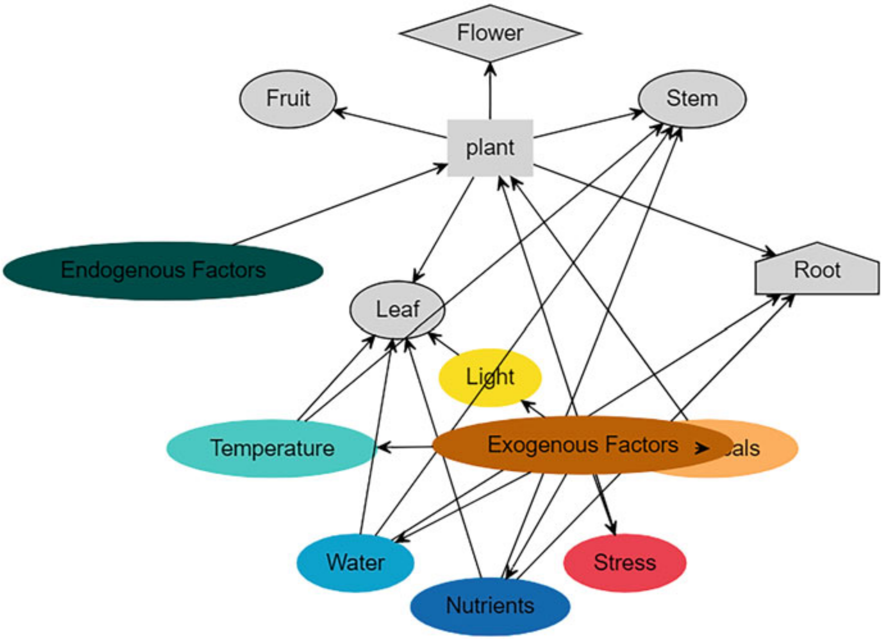

Fig. 3.1 The cluster graph showing clusters of plant parts and factors affecting melatonin production in plants. **Description of the diagram:** The "cluster_plant" subgraph contains five nodes that represent different parts of a plant: "root," "stem," "leaf," "flower," and "fruit." The "cluster_factors"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

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

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

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

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

3.6 Conclusion and Future Directions

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

3.6.1 Summary of the Key Findings

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

3.6.2 Future Research Directions

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

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

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

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

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

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Regulatory Role of Melatonin in Flowering, Fruit Setting, and Ripening

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Abstract

Role of melatonin in vertebrates and plant growth and metabolism is well evident now. Melatonin is a non-toxic biological substance (N-acetyl-5-methoxytryptamine), synthesized naturally in the pineal gland of animals, whereas tissues (leaves, fruits, stems, roots, and seeds) of various plant parts. It plays a crucial role in the plant immune response along with other important chemicals like nitric oxide and various hormones like salicylic acid and jasmonic acid. Plant releases melatonin in response to both abiotic (elevated soil salinity, variations in temperature, drought, toxins, etc.) and biotic (fungal infection) stress conditions. In fruit and vegetable crops, melatonin is widely involved in physiological and biological processes at both pre-harvest and postharvest stage. These

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include plant growth, flowering, germination of pollen, enhance fruit production, rhizogenesis, senescence, and postharvest preservation. Apart from this, it plays an important role in improving cell–water relationship, photosynthesis, primary and secondary metabolism, CO_2 uptake, etc. It is also reported that melatonin is associated with majority of other plant hormones. Melatonin triggers the production of pathogenesis-related proteins, which bolster the plant's defence against pathogens, and antioxidant enzymes, which help neutralize harmful reactive oxygen species produced during stress. This chapter highlights the regulatory role of melatonin in the context of its pre-harvest (flower development, flowering, and fruit setting) as well as postharvest influence (fruit development and fruit ripening) on fruit and vegetables.

Keywords

Melatonin · Biological substance · Flowering · Fruit setting · Parthenocarpy · Fruit ripening

4.1 Introduction

In the living kingdom, melatonin is a widely distributed biomolecule having pleiotropic effects. Melatonin (N-acetyl-5-methoxytryptamine) is an indoleamine that shows structural similarity with other indoleamine compounds such as auxin, tryptophan, serotonin, and others. Melatonin is a pervasive biomolecule with a wide range of effects throughout the living kingdom, and it belongs to the group of indoleamine compounds. Its chemical name is N-acetyl-5-methoxytryptamine and shares a structural similarity with other important indoleamine compounds, such as tryptophan, auxin, and serotonin (a neurotransmitter and hormone in animals) (Sharif et al. 2022). Other than its structural similarity with other indole amine compounds, melatonin and auxin share a common precursor, tryptophan, and have a similar biosynthetic pathway (Gao et al. 2022). It is produced through the catalysis of tryptamine-5 hydroxylase, N-acetyl-5 hydroxytryptamine-methyltransferase tryptophan decarboxylase, and 5-hydroxy tryptamine-N-acetyltransferase, which results in the catabolization to 2-hydroxymelatonin (Nawaz et al. 2020). It usually occurs in the mitochondria and chloroplast of the leaves and roots of plants and is then transmitted to the flowers, meristem, and fruits (Wang et al. 2016; Nawaz et al. 2020). Melatonin has a profound impact on various physiological systems in both animals and plants such as sleep, circadian rhythms, the immune system, and body temperature (Manzoor et al. 2023). Additionally, it plays a very important role in various cellular processes as an antioxidant and has outstanding free radical scavenger activities both in vitro and in vivo (Sun et al. 2021; Ze et al. 2021; Ahammed and Li 2022). The role of melatonin as a plant growth regulator (PGR) in seed germination, root development, blooming, fruit setting, and ripening has been extensively studied in plants (Gao et al. 2022). Additionally, postharvest fruit's quality and shelf life can both be enhanced by melatonin (Ze et al. 2021).

Its capacity to provide resistance to many biotic and abiotic stressors, including microbial infections (fungi, bacteria, and viruses) (Zhang et al. 2017), cold (Jayarajan and Sharma 2021; Li et al. 2021), salinity, drought, and high temperatures (Moustafa-Farag et al. 2020) has been noticed. Melatonin has been shown in recent research to be effective in lowering the accumulation of heavy metals and pesticide residues in foods (Yan et al. 2019; Gao et al. 2022). These qualities make melatonin a compelling contender to increase the development of horticulture crops and ensuring food safety (Nawaz et al. 2020).

This chapter highlights the regulatory role of melatonin in context to its pre-harvest (development of flower, flowering, and fruit setting) as well as postharvest influence (fruit development and fruit ripening) on fruit and vegetables.

4.2 Regulatory Role of Melatonin in Flowering

4.2.1 Influence of Melatonin on Flowering of Crops

Melatonin accumulation in flowers serves a protective role, shielding the various reproductive tissues from several abiotic stresses like more light intensity and low temperatures and this protection is especially crucial during the vulnerable stages of a plant's life cycle (Park et al. 2013; Tiwari et al. 2021). The timing of harvest and the yield are greatly impacted by flowering. Flowering has a big impact on when to harvest and how much of a yield forms (Gao et al. 2022). When fruit trees are in the late spring flowering stage, they frequently encounter cold spells. In order to prevent blossoms on fruit trees from being damaged by freezing during these cold spells, flowering time should be postponed (Gao et al. 2022). Melatonin levels in apple trees always dropped when the trees started to blossom, according to Zhang et al. (2019). Prior to the germination of the mixed bud, 'Fuji' apple trees were treated with various conc. of melatonin, i.e., 0, 20, 200, and 1000 μM. Melatonin treatments at 20 and 200 μM delayed flowering in apple by 2 days in compared to the control, while high conc., i.e., 1000-μM, postponed flowering by 3 days (Mou et al. 2022). Melatonin exogenously applied at 20 and 200 μM enhanced flowering rates by 63.8 and 72.7%, respectively, over the control (57.4% blooming rate). Transgenic *Oryza sativa* plants were able to prolong blooming by 1 week when endogenous melatonin levels were high (Mou et al. 2022). Previous reports on the potential role of melatonin in regulation of flowering used the short-day plant *Chenopodium rubrum*. These studies revealed that flower induction was reduced by an average of 40–50% when high amounts of melatonin were used between 2 h before and 2 h after the start of the inductive dark phase (Kolar et al. 2003; Park 2011). CGP-52608 (1-[3-allyl-4-oxothiazolidine-2-ylidene]-4-methyl-thiosemicarbazone) was discovered to be a potent melatonin antagonist that effectively prevents flower induction. Melatonin application, however, had no impact on the flowering stage, indicating that it controlled a mechanism taking place before the flowers changed. In a parallel experiment, melatonin concentrations of 100 or 500 μM affected anthesis, leaf and rosette counts, and flowering in the long-day plant (LDP) *Arabidopsis thaliana.*

Similar research in the long-day plant *Arabidopsis thaliana* revealed that flowering was somewhat postponed in plants when they were treated with various conc. of melatonin, i.e., 100 or 500 µM, which had an effect on anthesis, number of leaves, and rosettes (Arnao and Hernandez-Ruiz 2020). Devil's trumpet (*Datura metel*), a highly addictive plant, produced the most melatonin as its flower buds grew, which is utilized in natural medicine all over the world. This finding suggests melatonin had a protective effect on reproductive tissue (Murch et al. 2009; Arnao and Hernandez-Ruiz 2020).

4.2.2 Role of Melatonin on the Yield Potential of Crops by Influencing Flowering

The melatonin accumulation in flowers provides protection to the reproductive organs from different abiotic stresses, like more light intensity and cold stress, at the most crucial and vulnerable stages of a plant's life cycle (Murch et al. 2009; Aghdam et al. 2019; Sun et al. 2021). A field-grown rice plant's melatonin levels were measured at the plant's pre-flowering, flowering, and post-flowering stages of reproduction. The panicle (flower) was discovered to have a sixfold higher rate of melatonin production than the flag leaves. Melatonin may be implicated in floral development as this induction coincided with the induction of melatonin biosynthesis enzymes (Park et al. 2013). According to the studies, in Arabidopsis, which lacks ascorbic acid, melatonin may help regulate time of flowering in a manner comparable to that of ascorbic acid. The scientists speculate that melatonin may regulate time of flowering in a same manner to how ascorbic acid does in the ascorbic acid-deficient plant Arabidopsis. An ascorbic acid-rich mutant had delayed flowering, whereas the Arabidopsis mutant had an early flowering phenotype (Fig. 4.1). Levels of ascorbic acid and probable hormonal and changes in metabolites have been linked, even if the results do not conclusively correlate flowering to the antioxidant status of tissues (Kotchoni et al. 2009). Additionally, phenotypes of melatonin-rich transgenic plants overexpressing sheep serotonin N-acetyltransferase (SNAT) exhibited a biomass increase of twice and an endogenous melatonin content that was three times higher than that of wild-type plants in rice plants grown in field conditions. Flowering took a week longer in the transgenic strains. The grain yield of the transgenic lines with high melatonin levels was on average 33% lower. This opens up new opportunities to use melatonin to boost crop yields by regulating flowering time and extending the harvest season (Gao et al. 2022).

In *Arabidopsis thaliana,* the ambient temperature, photoperiod, gibberellic acid, age pathways, vernalization, and autonomous are among the at least 6 distinct signalling flowering pathways. A MADS box-containing transcription factors (TFs) that bind to the promoters of flowering locus T (FT) and suppressor of overexpression of ConstanS1 (SOC1) to inhibit floral transition are encoded by the crucial autonomous pathway gene flowering locus C (FLC). Both squamosa promoter-binding protein-like (SPL) and FLC, which act as GA signalling antagonists, encode for proteins connected to the DELLA proteins (Fig. 4.2).

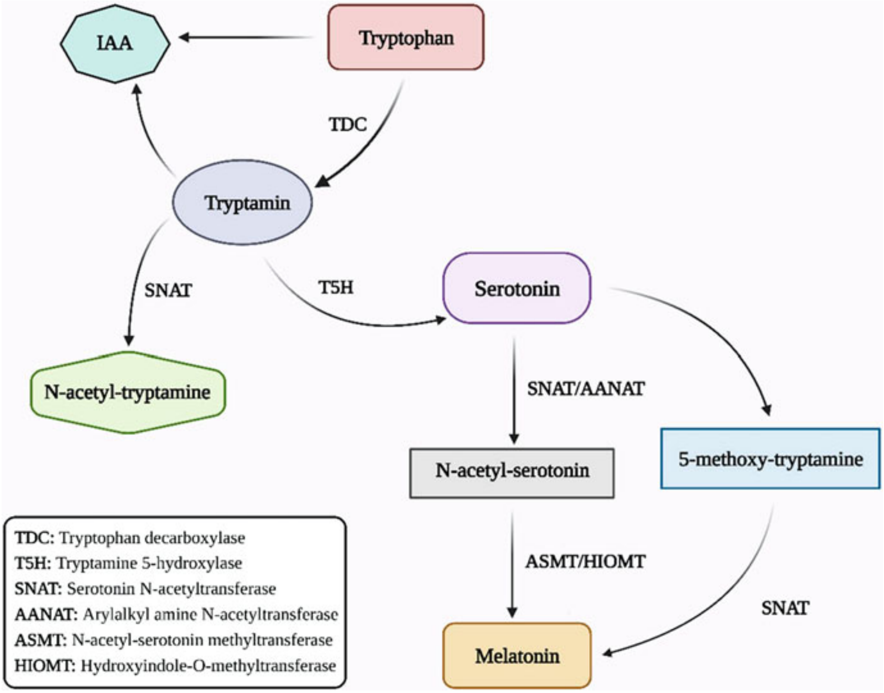

Fig. 4.1 Schematic pathway of melatonin expression

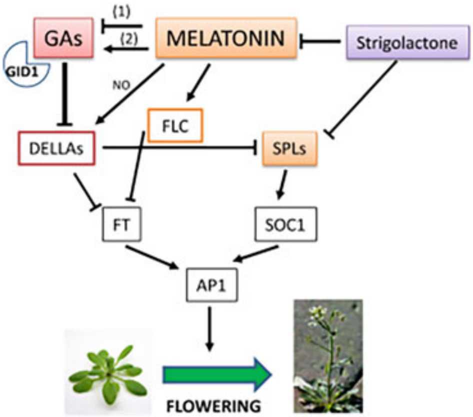

Fig. 4.2 Melatonin role in flowering. Melatonin slows down Arabidopsis flowering through controlling the expression of FLC, GA, and DELLA. Strigolactone works by impairing the production, signalling, and SPLs of melatonin, resulting in early flowering. *FLC* flowering locus C (core repressor of vernalization), *SOC1* suppressor of overexpression of Constans 1, *GID1* GA receptor, *SPL* Squamosa promoter-binding protein-like, *FT* flowering locus T, *DELLAs* transcriptional repressors of GA responses, *API1* Apetala1

Researchers have described the relationships between phytomelatonin and other phytohormones (Khan et al. 2022). According to the scientists, strigolactones (SLs) function upstream of melatonin to postpone flowering because they activate FLC when the amount of melatonin in plant tissues exceeds a particular threshold. It is interesting to note that NO, whose synthesis is melatonin-stimulated, raises DELLA protein levels and prevents the transition of flower in Arabidopsis (Sun et al. 2021). Shi et al. (2016) initially identified the direct relationship between floral transition and melatonin and hypothesized that NO may have a role in the melatonin-stimulated stabilization of DELLA proteins, which results in a definite late flowering.

4.3 Regulatory Role of Melatonin in Fruit Setting

4.3.1 Melatonin Influences Fruit Setting

The crucial role of melatonin in fruit set and development has been the subject of numerous investigations (Arnao and Hernandez-Ruiz 2020). Around 10–15 days after anthesis in the developing ovule, when the early stages of seed development were taking place, melatonin levels in *Datura metel* fruits significantly increased over the course of fruit growth (Park 2011). Veraison, which is marked by softening of berries and a quick rise in weight of seed, is when wine grapes produce the most melatonin. According to these results, the rise in melatonin levels during a specific stage of fruit development may act as a transitional signal for seed growth (Murch et al. 2010). The greatest contents of melatonin were identified during II stage of fruit development of cherry *(Prunus avium*), growth of embryo, and lignification of endocarp, which has also been connected to reactive oxygen species generation in “watery” seeds, suggesting that rapid biosynthesis of melatonin increased by oxidative stress (Arnao and Hernandez-Ruiz 2020). More concentration of melatonin has been found in the flowers, as well as immature and mature red fruits and seeds of two pepper (*Capsicum annuum*) cultivars. The amount of melatonin in both fruit and seeds considerably enhanced as the fruit and, consequently, seeds developed. The authors find that the higher levels of melatonin found in both cultivars’ reproductive organs, mature fruits, and seedlings at the cotyledon stage are evidence that these organs are being protected from adverse environmental conditions due to the higher levels of melatonin (Korkmaz et al. 2014). Micro-Tom tomato fruits have been found to contain melatonin throughout the fruit’s growth, with the fruit’s highest concentration occurring in the final stages, when the fruits take on a pink-red tint (Arnao and Hernandez-Ruiz 2020). The fact that seeds of tomato were containing maximum concentration of melatonin is interesting because it shows that melatonin in seeds may have a protective function, as was previously suggested. The highest values were seen during uninucleate development in *Hypericum perforatum.* According to Murch and Saxena (2002), isolated anthers had a better regeneration capability when melatonin levels were high. The expression of melatonin biosynthesis genes is perfectly synchronized with melatonin production in the growth of red Fuji apple fruits (*Malus domestica*). Malondialdehyde, a byproduct of lipid peroxidation, and the amount of melatonin in fruits showed an inverse association. Two significant melatonin peaks emerged during fruit development, which coincided with the fruits' rapid growth and an increase in respiration and ROS (Lei et al. 2013). In a study of tomato fruits, serotonin content, a precursor to melatonin, increased during fruit development in all fruit tissues (mesocarp, exocarp, placenta, columella, seed and jelly), reaching a maximum in the completely ripe stage (Arnao and Hernandez-Ruiz 2020). In comparison to leaves, stems, or flower heads, mature hemp (Cannabis sativa) plant seeds contain 4–10 times more melatonin (Allegrone et al. 2019). In any event, it is still not apparent if melatonin peaks are a sign of fruit growth or a defence mechanism to keep fruits and seeds' proper redox status while they are developing.

4.3.2 Melatonin Influences Fruit Development and Parthenocarpy

The development of fruit without fertilization of ovule is known as parthenocarpy and can occur naturally or artificially. Auxin and gibberellins, two plant hormones, can cause parthenocarpy in a variety of horticulture species (Srivastava and Handa 2005). Melatonin stimulates parthenocarpy in the Starkrimson pear (*Pyrus communis*) by boosting GA_3 and GA_4 production, resulting in development of fruits that resemble those produced by hand pollination through fruit cell proliferation and enlargement of mesocarp (Liu et al. 2018a). Exogenous melatonin treatment caused the seeds of the fruit to develop abnormally and abortion during fruit setting. According to the research, the fruit shape index dramatically increased, the transverse diameter of the fruit dropped, and the longitudinal diameter definitely increased, all effects that are identical to those of GA treatment (Arnao and Hernandez-Ruiz 2020). The outcome of this research revealed that the ovaries' GA_3 and GA_4 levels enhanced, the fruit shape index raised noticeably, the transverse diameter of the fruit reduced, and the longitudinal diameter obviously widen, all effects that were identical to those of GA application. Melatonin significantly raised the level of active GAs by upregulating GA20ox (which creates active GAs) and downregulating GA2ox (which produces inactive GAs). Comparatively, the IAA content decreased after pollination compared to the control, and neither the IAA content nor the number of seed cell layers in the ovary increased following melatonin application. These findings conflict with those obtained using eggplant parthenocarpy induced by IAA (Arnao and Hernandez-Ruiz 2020). Melatonin application had little effect on auxin-signalling-related genes, demonstrating that IAA is not a significant contributor to pear parthenocarpy. Genes associated with photosystems I and II, carbohydrates, and chlorophyll showed increased expression following melatonin application. The number of genes connected to the cell cycle and growth of cell was altered by treatment of melatonin, according to transcriptome data. Plant cyclins and expansins perform crucial functions in plant development and cell division (Choi et al. 2006).

4.4 Regulatory Role of Melatonin in Fruit Ripening and Senescence

4.4.1 Postharvest Losses in Fruit and Vegetables Due to Improper Ripening and Senescence

The postharvest losses occur approximately 20–40% in various fruits and vegetables (Prasad et al. 2018a), which takes place at several stages of postharvest handling, i.e., fruit characteristics (Saroj and Prasad 2023; Prasad et al. 2020), harvesting (Prasad et al. 2019), transportation, storage (Prasad et al. 2016), marketing (Prasad et al. 2018a, 2022a), and ripening/senescence management (Prasad et al. 2020). Hence, it is crucial to use postharvest management techniques that are both effective and efficient when managing fresh horticultural produce (Prasad et al. 2022a, b). These include proper harvesting method (Prasad et al. 2019), pre-cooling, sorting, grading, packaging, and storage (Prasad and Sharma 2018; Prasad et al. 2022b). Many postharvest techniques have been proposed to mitigate chilling injury, physiological disorders (Prasad and Sharma 2016), minimizing decay (Prasad et al. 2016), thereby control ripening which ultimately enhances shelf life of the produce (Prasad and Sharma 2018; Prasad et al. 2018b). Melatonin is an emerging postharvest molecule in this context (Jayarajan and Sharma 2021).

4.4.2 Regulatory Role of Melatonin in Fruit Ripening

Numerous researches have revealed that exogenous melatonin increased the amount of natural melatonin in fruits after harvesting. The level of endogenous melatonin in banana fruit was increased by exogenous melatonin, and similar results were shown in litchi (*Litchi chinensis*), sweet cherries and tomato (Wang et al. 2020). This effect is brought about by melatonin activating the shikimic acid pathway, which causes a buildup of aromatic amino acids and, in turn, increases the synthesis of melatonin (Aghdam et al. 2019; Wang et al. 2020). Fruit firmness was retained in pear, banana, and mango after exogenous melatonin application because the activities of enzymes involved in starch and cell wall degradation were blocked (Ze et al. 2021). Fruit colour was also considerably delayed in mango, kiwifruit, and banana. After melatonin treatment, the qualitative characteristics of various fruits, such as soluble sugars, carotenes, weight loss, respiration rate, organic acids, volatile aroma, and titratable acidity can be maintained to a large extent (Ze et al. 2021).

The fundamental factor controlling fruit ripening is ethylene production, but ethylene and antioxidants such as organic acids and phenolic substances also limit senescence. According to the literature, melatonin may have some influence over the speed at which fruit ripens, although the exact mechanism by which it does this is yet unknown. Melatonin when applied externally, positively regulated production of ethylene and signalling, which in turn stimulated the ripening of tomato after harvest and brought about biochemical changes such as volatiles biosynthesis, production of lycopene and carotenoid and cell wall breakdown (Jayarajan and Sharma 2021)

Table 4.1 Effect of melatonin treatment on fruit ripening

Fruit	Melatonin concentration	Effect	References
Tomato	50 µM	Upregulating the expression of the gene for colour development, ethylene production improved postharvest shelf life and encouraged ripening	Jayarajan and Sharma (2021)
'Moldova' grape	100 µM	Enhanced ripening via controlling abscisic acid signalling	Jayarajan and Sharma (2021)
Banana	200, 500 µM	Postponed the ripening after harvest. By controlling the expression of the MaACO1 and MaACS1 genes, endogenous amount of melatonin was increased, which in turn decreased the generation of ethylene	Hu et al. (2017)
Strawberry	100 µM	Enhanced activities of antioxidants enzymes, phenolics, total antioxidant	Aghdam and Fard (2017) and Liu et al. (2018b)
Peach	0.1 mM, 10 min	Delayed ripening	Gao et al. (2016)
Jujubes	100 µM	Application of melatonin slowed down colour variations and encouraged the synthesis of phenolic chemicals	Wang et al. (2021)

Musa acuminata 1-aminocyclopropane-1-carboxylic acid oxidase 1, *MaACS1 Musa acuminata* 1-aminocyclopropane-1-carboxylic acid synthase 1

(Table 4.1). Exogenous melatonin lowered the production of ROS in a variety of fruits and hence delayed fruit ripening by boosting the enzymatic activity and gene expression of antioxidant enzymes (Onik et al. 2020; Wang et al. 2020). At a dosage of 100 µM, melatonin significantly enhanced the contents of ABA, H_2O_2, and production of ethylene and accelerated the ripening of 'Moldova' fruit (Table 4.1). It is interesting to note that exogenous melatonin also increased endogenous melatonin levels, which decreased the synthesis of ethylene through controlling the expression of MaACS1 and MaACO1 genes and postponed abrupt changes in qualitative characteristics (Jayarajan and Sharma 2021). Hu et al. (2017) revealed how melatonin affected the quality and ripening of various banana types with various ripening times. They discovered that exogenous melatonin treatment considerably slowed postharvest ripening in all varieties at concentrations of 200 or 500 µM. Prunus domestica plums were submerged in a different concentrations of melatonin solutions at 1 °C for 40 days and observed that the 0.1- and 1-mM solutions of melatonin worked best for halting weight loss and preserving better firmness. Arnao and Hernandez-Ruiz (2020) examined that, melatonin-treated plums had higher ascorbic acid concentration, antioxidant activity and total phenolic content, than the control. Additionally, strawberries (Aghdam and Fard 2017; Liu et al. 2018b), grapes (Meng et al. 2015), peaches (Gao et al. 2016), and jujubes (Wang et al. 2021) have all benefited from melatonin treatment in terms of postharvest quality and life.

4.4.3 Regulatory Role of Melatonin in Fruit Senescence

By blocking biosynthesis of ethylene through nitric oxide regulation, inhibiting biosynthesis of ABA, chlorophyll degradation, increasing ascorbic acid, total phenol content, controlling membrane lipid, energy metabolism, melatonin showed good performance in postponing senescence of fruit and vegetable (Wang et al. 2020; Wu et al. 2021). Broccoli heads treated with melatonin (100 L/L) displayed increased antioxidant activity, greater vitamin C and total carotenoids protection, and higher antioxidant activity. According to Jayarajan and Sharma (2021), it also prevented broccoli from yellowing by 4 days compared to the control, which is a major obstacle to broccoli marketing. Similar to this, melatonin-treated pears showed decreased production of ethylene, improved firmness, reduced senescence, over the course of storage compared to control fruits. In three different cultivars on pear, i.e., “Starkimson,” “Abbe Fetel,” and “Red Anjou,” the treatment blocked the expression of the genes PcACS1 and PcACO1 which are responsible for ethylene biosynthesis as well as gene which is responsible for the cell wall degradation (PcPG). Aside from that, the treated pear fruits had a high AOX capacity and showed no signs of water core or core browning (Zhai et al. 2018).

4.5 Conclusion

Melatonin may actively influence the growth of flowers and fruits, as well as fruit set, ripening, and senescence. It has been suggested that stresses like light and temperature can prevent flowering. The direct link between the stimulation of melatonin producing enzymes and melatonin peak(s), however, raises the possibility that it plays a very important role in flower development. The most important function of melatonin during fruit set is its capacity to trigger parthenocarpy. Ripening of fruit is accelerated and their senescence is postponed by melatonin. The potential use of melatonin to delay flowering needs additional research in terms of future prospects. More information on the interactions between melatonin and phytohormones is critical with regard to the fruit set.

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Regulatory Role of Melatonin in Photosynthesis and Respiration

5

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Abstract

Melatonin is a hormone that has recently been identified as playing a key role in photosynthesis and respiration in plants. Its effects are primarily mediated through its ability to regulate the light-dependent processes of photosynthesis, as well as its ability to modulate respiration rates. Specifically, melatonin has been observed to enhance photosynthetic efficiency, as well as increase the rate of respiration in plants. Melatonin appears to have a role in regulating the circadian rhythm of plants, allowing them to respond properly to day and night cycles. In photosynthesis, melatonin appears to act as an antioxidant, protecting plants from photodamage and increasing the efficiency of photosynthesis. Its antioxidant properties also protect plants from oxidative damage induced by environmental factors, such as high temperatures and ultraviolet radiation. Melatonin has been observed to increase the chlorophyll content of plants, which further increases

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photosynthetic efficiency. Melatonin also appears to play a role in regulate the rate of respiration in plants. Studies have found that melatonin increases the rate of respiration in plants, allowing them to take in more oxygen and release more carbon dioxide, thereby increasing their overall respiration efficiency. Future research should focus on further elucidating the role of melatonin in photosynthesis and respiration in plants. Understanding how melatonin impacts these processes could provide valuable insights into the regulation of photosynthesis and respiration in plants and how these processes are affected by environmental factors. Investigating the potential use of melatonin as a plant growth regulator could potentially lead to the development of new strategies for improving crop production.

Keywords

Antioxidant · Photosynthesis · Oxidative stress · Hormones · Enzymes · Crop production · Growth regulator

5.1 Introduction

Melatonin is a hormone produced in plants and animals that is involved in regulating circadian rhythms and sleep. It is produced by the pineal gland in mammals and plays a major role in the regulation of the body's sleep–wake cycles. It is also found in plants, algae, and fungi, where it is thought to have a role in photoperiodism, the process by which plants adjust their growth and flowering cycles in response to changes in day length (Back et al. 2016). In plants, melatonin is synthesized from the amino acid tryptophan using the enzyme serotonin N-acetyltransferase (SNAT). It is released during the day and accumulates in the plant's tissues overnight (Fig. 5.1). During the day, the plant uses the accumulated melatonin to regulate its internal processes and growth (Zhao et al. 2019).

Melatonin is a hormone that plays an important role in regulating the circadian rhythm of plants. It is produced in the chloroplasts of plants and acts as a regulator of photosynthesis and respiration (Behera et al. 2022; Chourasia et al. 2022; Kumar et al. 2022a, b). Melatonin has been found to be an important factor in the regulation of light-mediated responses in plants, such as photosynthesis, stomatal opening and closing, and photoperiodism (Tan et al. 2012; Arnao and Hernández-Ruiz 2018). The study of the role of melatonin in plants is relatively new, but a growing body of evidence suggests that it plays a significant part in the regulation of photosynthesis and respiration in plants.

Through photosynthesis, plants are able to generate the energy needed to grow and reproduce (Messinger and Shevela 2012). During photosynthesis, chlorophyll molecules absorb light energy and use it to produce sugar molecules. The sugar molecules then provide energy to the plant cells (Lal et al. 2022a, b; Altaf et al. 2022a, b, c, d). The process of photosynthesis is regulated by many factors,

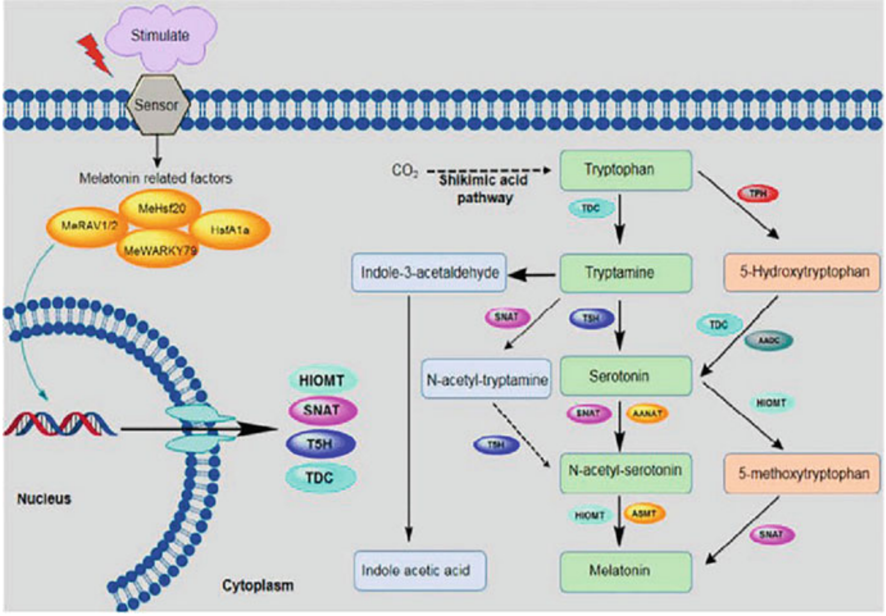

Fig. 5.1 Melatonin synthesis pathway in plants. *AADC* Aromatic L-amino acid decarboxylase, *ASMT* Acetylserotonin O-methyltransferase, *COMT* Catechol-O-methyltransferase, *SNAT* Serotonin N-acetyltransferase, *T5H* Tryptamine 5-hydroxylase, *TPH* Tryptophan hydroxylase, *TDC* Tryptophan decarboxylase. (Source: Khan et al. 2020)

including light intensity, temperature, and the availability of water and nutrients (Barber 2009; Holding and Streich 2013).

The role of melatonin in the regulation of photosynthesis and respiration in plants is complex, but it is clear that it plays an important role in the process. Melatonin has been shown to affect the rate of photosynthesis in plants, particularly when the light intensity is low (Varghese et al. 2019). Studies have also shown that melatonin can increase the efficiency of photosynthesis by increasing the efficiency of the chloroplasts in converting light energy into chemical energy. In addition, melatonin has also been found to regulate the opening and closing of stomata, as well as the photoperiod sensitivity of plants (Szarka et al. 2013).

In particular, it is involved in the regulation of the light reactions of photosynthesis. This is the process by which light energy is converted into chemical energy. It is believed that melatonin helps to coordinate the activities of photosystem II and photosystem I, two proteins involved in the light reactions of photosynthesis (Arnao and Hernández-Ruiz 2015; Wang et al. 2022a, b). Melatonin also helps to regulate the amount of light absorbed by plants. It has been found that plants exposed to light at night have a higher concentration of melatonin than plants exposed to light during the day (Tiwari et al. 2022a, b). This suggests that melatonin helps to regulate the amount of light absorbed by the plant (Teng et al. 2022).

Recent studies have shown that melatonin can directly regulate respiration in plants. In a study on Arabidopsis thaliana, melatonin was found to decrease respiration activity in the plant, likely mediated through the inhibition of mitochondrial respiration (Wang et al. 2022a, b). Additionally, melatonin was observed to increase the activity of alternative respiratory pathways, such as glycolysis and the pentose phosphate pathway. In this way, melatonin can effectively regulate respiration in plants (Sharif et al. 2018). Melatonin can also act as a signal molecule to modulate respiration in plants in response to environmental cues. For example, melatonin has been found to increase respiration activity under conditions of low temperature, drought, and other stress factors. This increase in respiration activity may serve to boost the plants' energy production, allowing it to better cope with the stressful environment (Antoniou et al. 2017; Gu et al. 2021; Lal et al. 2022c). Melatonin has also been observed to be involved in the regulation of photosynthesis in plants. It has been shown to increase the light-dependent photosynthetic rate and the chlorophyll content in plants. These effects are likely mediated through the modulation of respiration and stomatal opening (Teng et al. 2022; Wang et al. 2022a, b).

Melatonin is also thought to play a role in the regulation of the circadian rhythms in plants, such as the timing of flowering, leaf movement, and seed germination. It has been shown to stimulate the production of certain hormones and enzymes, as well as to modulate the response of plants to environmental stressors (Kumar et al. 2022a; Lal et al. 2022d). In addition, studies have suggested that melatonin may be involved in the regulation of certain metabolic pathways and may even serve as an antioxidant. While much is still not known about how melatonin works in plants, it is clear that it plays an important role in regulating their growth and development. It is also thought to be involved in a variety of stress responses and in the regulation of certain metabolic pathways. As such, it is a topic of ongoing research and is likely to continue to be studied in the future.

5.2 Role of Melatonin in Photosynthesis

Melatonin does not play a direct role in photosynthesis. However, it does play an indirect role because it helps to regulate the circadian rhythms of plants, which in turn can affect photosynthesis. For example, melatonin helps plants to adjust to changing light/dark cycles by regulating the timing of stomatal opening and closing (Fig. 5.2). This helps plants to optimize their photosynthesis and make the most efficient use of available light. Additionally, melatonin can help to protect plants from oxidative stress caused by light, which can reduce the efficiency of photosynthesis (Debnath et al. 2018; Ahmad et al. 2021).

The role of melatonin in photosynthesis activity is explained by different ways:

5.2.1 How Melatonin Influences Photosynthesis?

Melatonin has been found to play a role in photosynthesis by influencing the activity of the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), the

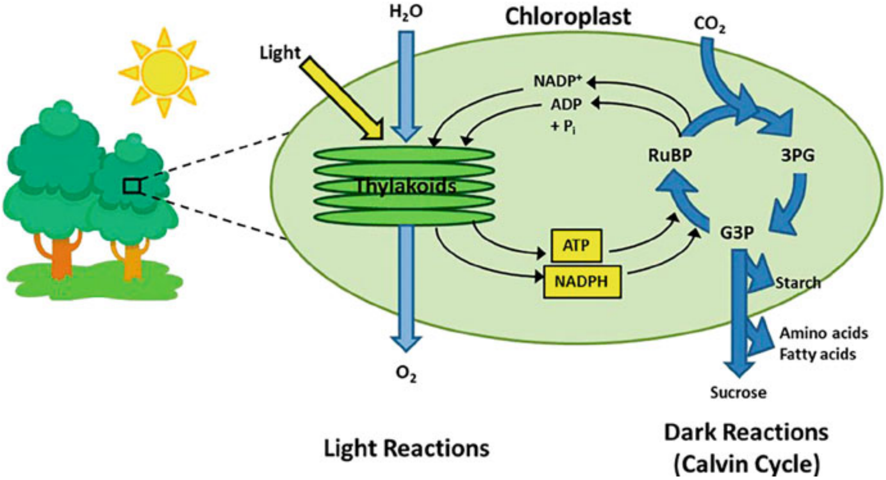

Fig. 5.2 The photosynthesis process in plants. *NAD+* Nicotinamide Adenine Dinucleotide (oxidized form), *NADP* Nicotinamide adenine dinucleotide phosphate (oxidized form), *ATP* Adenosine triphosphate, *NADPH* Nicotinamide adenine dinucleotide phosphate (reduced form), *G3P* Glyceraldehyde 3-phosphate, *Pi* Inorganic phosphate, *RuBP* Ribulose-1,5-bisphosphate. (Source: Rasmussen and Minteer 2014)

main enzyme responsible for carbon fixation. Studies have shown that melatonin increases the activity of RuBisCO in plant cells, which in turn increases the rate of photosynthesis. This increased photosynthesis leads to greater plant growth and productivity (Talaat 2021). Additionally, melatonin helps protect plant cells from oxidative stress that can be caused by excessive light exposure. This protection helps maintain the health of plants and ensures efficient photosynthesis (Liang et al. 2019).

In addition to its influence on RuBisCO, melatonin has also been found to protect plant cells from the damaging effects of excessive light exposure (Table 5.1). Exposure to high levels of light can cause oxidative stress, which can damage the cells and reduce their ability to photosynthesize (Xu et al. 2016; Zuo et al. 2017). However, melatonin has been found to act as an antioxidant, helping to neutralize the oxidative stress caused by excessive light and thus protecting the plant cells from damage (Xie et al. 2022).

Furthermore, melatonin has also been found to help plants adjust to changing light conditions. When exposed to different levels of light, plants adjust the activity of their photosynthetic enzymes, including RuBisCO, to ensure that their cells are able to photosynthesize efficiently (Bychkov et al. 2019). Melatonin has been found to help facilitate this process, allowing plants to adjust to changing light conditions and maintain efficient photosynthesis (Fig. 5.3).

It is an antioxidant that can help protect plant cells from damage caused by exposure to UV light. It also helps regulate the circadian rhythm of plants and can help to promote optimal photosynthetic activity (Tan et al. 2012; Reiter et al. 2013). Melatonin can also help plants to regulate their water use, as well as their responses

Table 5.1 Effect of melatonin in regulation of photosynthesis in different crops

Crop	Amount of melatonin	Regulation of photosynthetic activity
Maize	0.7 μg/g	• Increased photosynthetic efficiency • Help regulate the production of abscisic acid
Rice	1.1 μg/g	• Opening and closing of stomata • Production of auxins
Soybean	0.5 μg/g	• Regulate the production of gibberellins • Production of gene expression
Tomato	0.8 μg/g	• Help regulate the production of abscisic acid
Wheat	1.2 μg/g	• Opening and closing of stomata • Production of auxins
Cucumber	0.5 μg/g	• Production of auxins
Potato	0.9 μg/g	• Help regulate the production of gibberellins • Control opening and closing of stomata
Onion	0.7 μg/g	• Regulate the production of gibberellins • Regulate the enzymes for photosynthesis
Barley	1.0 μg/g	• Opening and closing of stomata • Production of auxins

(Source: Arnao and Hernández-Ruiz 2015; Zhou et al. 2016; Varghese et al. 2019; Tiwari et al. 2021)

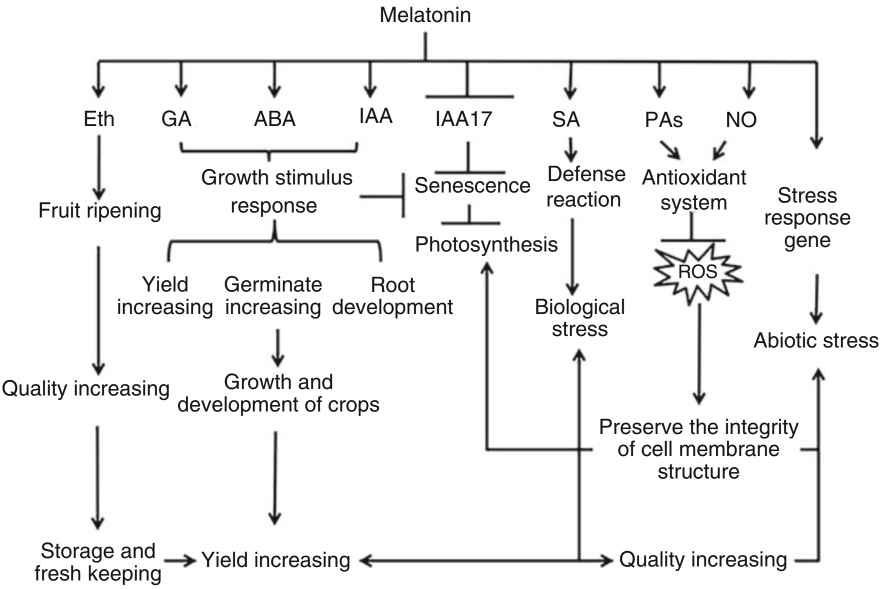

Fig. 5.3 Overall role of melatonin in crops. *ABA* Abscisic acid, *Eth* ethylene, *GA* Gibberellins, *IAA* Indole-3-acetic acid, *PAs* polyamines, *ROS* reactive oxygen species. (Source: Yan et al. 2020)

to environmental stresses like drought and high temperatures. It can also act as a signaling molecule to help coordinate the growth and development of plants (Zhang et al. 2015; Tiwari et al. 2020).

Examples:

The role of melatonin is important in all crops related to food, feed, and fodder. Here are some important crops where melatonin is playing important role.

5.2.1.1 Maize (*Zea mays* L.)

Melatonin has been found to have a number of effects on photosynthesis in maize. Melatonin has been shown to increase the efficiency of photosynthesis by improving the efficiency of electron transfer in the photosynthetic electron transport chain. This increased efficiency leads to an increase in the amount of energy produced per photosynthetic reaction, leading to an increase in the amount of biomass produced by the plant (Ahmad et al. 2021).

It has been found to increase the amount of chlorophyll in the plant. Chlorophyll is the pigment responsible for absorbing sunlight and converting it into energy. When there is an increase in the amount of chlorophyll in the plant, there is an increase in the amount of light absorbed and, therefore, an increase in the amount of energy produced by the plant (Ahmad et al. 2022).

Finally, melatonin has been found to increase the activity of the enzyme Rubisco, which is responsible for the reaction of carbon dioxide and ribulose-1,5-bisphosphate to produce 3-phosphoglycerate. This reaction is essential for the production of energy from photosynthesis. Therefore, an increase in the activity of Rubisco leads to an increase in the rate of photosynthesis and the amount of energy produced (Wang et al. 2021).

5.2.1.2 Wheat (*Triticum aestivum*)

Wheat is a cereal grain and one of the most important crops in the world. It is a major source of carbohydrates, proteins, and other nutrients for humans. Photosynthesis is the process by which plants use energy from sunlight to convert carbon dioxide and water into energy-rich compounds such as glucose (Knör 2015).

Melatonin is synthesized in wheat by the enzyme serotonin N-acetyltransferase (SNAT), which is located in the chloroplasts. In wheat, melatonin is found in the leaf and stem tissue, as well as in the grains. It is believed that melatonin may influence photosynthesis in wheat by regulating the activity of certain enzymes involved in the process (Turk et al. 2014; Talaat 2021).

Recent studies have shown that melatonin affects the expression of certain genes related to photosynthesis. For example, melatonin has been shown to increase the expression of photosynthesis-related genes such as rubisco, photorespiratory enzymes, and others (Wang et al. 2013). It is thought that melatonin may also regulate the rate of photosynthesis by modulating the activities of various enzymes involved in the process. In addition, melatonin has been shown to affect the rate of photosynthesis in wheat by influencing the activity of certain hormones involved in the process. For example, melatonin has been shown to reduce the level of abscisic acid, a hormone involved in the regulation of photosynthesis (Zhang et al. 2020; Li et al. 2021; Hu et al. 2022). Moreover, melatonin can also increase the levels of auxin, a hormone that stimulates the growth of young plants (Pelagio-Flores et al. 2012). Melatonin can increase the uptake of carbon dioxide by the wheat plants, which increases the efficiency of photosynthesis. In addition, melatonin can also increase the efficiency of the light-harvesting complexes, which are important for the production of energy from sunlight (Kul et al. 2019).

5.2.1.3 How Melatonin Enhances Photosynthesis in Plants?

Melatonin, an endogenous hormone, has been found to be beneficial in enhancing photosynthesis in plants. In the presence of melatonin, photosynthesis rate increases, leading to higher plant growth, increased seedling emergence, and increased fruit production (Table 5.2). It also helps in improving water and nutrient absorption, improving drought resistance, and improving overall plant health (Nawaz et al. 2020; Altaf et al. 2022a, b, c, d).

Melatonin plays an important role in the regulation of photosynthesis in plants. It acts as an antioxidant to protect the plants from the harmful effects of reactive oxygen species (ROS) created by the photosynthetic process (Fig. 5.4). The antioxidant property of melatonin can also reduce the damage caused by ultraviolet radiation (Goswami et al. 2013). In addition, melatonin also helps in the regulation of the redox balance of the plant, which is important for photosynthesis (Zhou et al. 2016). It helps in the activation of certain enzymes, such as ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and phosphoenolpyruvate carboxylase (PEPcase), which are essential for photosynthesis (Jahan et al. 2021; Siddiqui et al. 2022; Wang et al. 2022a, b). Melatonin also helps in the regulation of the Calvin cycle, which is the main process of photosynthesis (Zhao et al. 2022).

Melatonin also helps in the regulation of chlorophyll, which is essential for photosynthesis. Chlorophyll is important for absorbing light energy and converting it into chemical energy (Yang et al. 2022). Melatonin helps in the activation of enzymes involved in chlorophyll biosynthesis, which increases the amount of chlorophyll available for photosynthesis (Siddiqui et al. 2020). Moreover, melatonin

Table 5.2 Effect of melatonin in change in regulation of enzymes/protein and overall response on photosynthesis

Crop	Protein/enzyme affected by melatonin	Effect on photosynthesis
Wheat	Protein kinase C	Increases photosynthetic efficiency
Rice	G-protein-coupled receptors	Regulates chloroplast activity
Maize	Calcium-activated protease	Increases photosynthetic rate
Barley	MAPK-mediated signal transduction	Increases photosynthetic rate
Soybean	Phosphorylation of photosystem II	Increases photosynthetic efficiency
Potato	G-protein-coupled receptor	Regulates chloroplast activity
Tomato	Calmodulin-dependent protein kinase	Increases photosynthetic rate
Sorghum	Calcium-activated protease	Increases photosynthetic rate
Oat	Phosphorylation of photosystem II	Increases photosynthetic efficiency

(Source: Debnath et al. 2018; Sharma et al. 2020; Ahmad et al. 2021; Muhammad et al. 2022)

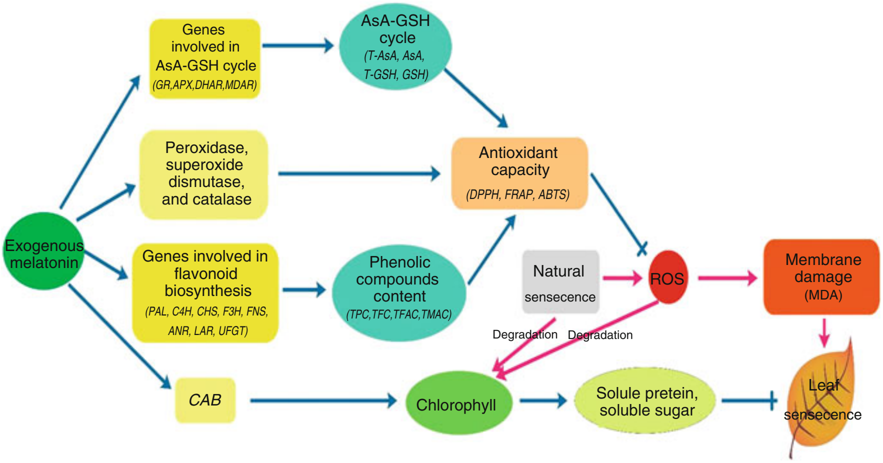

Fig. 5.4 Melatonin's role to increase photosynthesis activity and ripening. *ANR* Anthocyanidin reductase, *APX* Ascorbate peroxidase, *C4H* Cinnamate 4-Hydroxylase, *CAB* Chlorophyll A/B binding protein, *CHS* Chalcone synthase, *DHAR* Dehydroascorbate reductase, *F3H* Flavanone 3-hydroxylase, *GR* Glutathione reductase, *LAR* Leucoanthocyanidin reductase, *MDA* Malondialdehyde, *MDHAR* Monodehydroascorbate reductase, *PAL* Phenylalanine ammonia-lyase, *TFC* total flavonoid content, *TPC* total phenolic content, *UFGT* UDP-Glucose flavonoid 3-O-glucosyltransferase. (Source: Liang et al. 2018)

helps in the regulation of stomatal movements. Stomata are the small pores in the leaves of a plant that allow CO_2 to enter and O_2 to leave. Melatonin helps in the regulation of the opening and closing of the stomata, which is important for photosynthesis. The regulation of stomatal movements is important as it helps in controlling the amount of CO_2 entering the leaves and the amount of O_2 leaving the leaves (Li et al. 2015; Wang et al. 2023).

Examples:

(a) To illustrate, melatonin has been found to be beneficial in enhancing photosynthesis in tomato plants. In one study, melatonin was applied to tomato plants and it was found that the photosynthetic rate increased by 15%. This led to increased plant growth, increased fruit production, improved water and nutrient absorption, and improved drought resistance (Zhou et al. 2016).

(b) Another example is soybean plants. In a study, melatonin was applied to soybean plants and it was found that the photosynthetic rate increased by 8%. This led to increased seedling emergence, increased plant growth, and improved drought resistance (Zhang et al. 2019).

(c) Melatonin has also been found to be beneficial in enhancing photosynthesis in maize plants. In one study, melatonin was applied to maize plants and it was found that the photosynthetic rate increased by 12%. This led to improved water and nutrient absorption, increased plant growth, increased seedling emergence, and increased fruit production (Ye et al. 2016).

5.3 The Effects of Melatonin on Photosynthetic Productivity

Melatonin is a hormone found in both plants and animals that is known for its role in regulating sleep, but it can also have a major impact on photosynthetic productivity in crops. Melatonin has been found to have a variety of beneficial effects on photosynthesis, including increased chlorophyll and carotenoid synthesis, increased photochemical efficiency, increased photosynthetic rate, and increased photosynthetic product yield (Wang et al. 2022a, b).

Different crops have been found to benefit from melatonin when it comes to increasing their photosynthetic activity.

5.3.1 Wheat

Wheat is an important crop for its high gluten content and is widely used in baking and other food products. Studies have shown that melatonin can increase photosynthetic productivity in wheat by increasing chlorophyll and carotenoid levels, as well as increasing the photochemical efficiency of the photosynthetic process (Talaat 2021). In addition, melatonin can also increase the photosynthetic rate by increasing the availability of carbon dioxide to the plant. This increased photosynthetic rate can result in increased grain yields and improved grain quality (Iqbal et al. 2021; Khan et al. 2022a, b).

5.3.2 Rice

Rice is one of the most important crops in the world and is a staple food for many countries. Recent studies have found that melatonin supplementation can increase the photosynthetic efficiency of rice. The increased efficiency is due to increased photosynthetic activity and a decrease in the number of non-photosynthetic cells. This results in improved yields of rice (Zheng et al. 2017).

5.3.3 Soybeans

Soybeans are a popular crop for their high protein content and are widely used as animal feed and as a plant-based meat substitute. Studies have found that melatonin can increase photosynthetic productivity in soybeans by increasing the carotenoid and chlorophyll levels, as well as increasing the photochemical efficiency of the photosynthetic process (Fig. 5.5). This increased photosynthetic rate can result in increased grain yields and improved grain quality (Cao et al. 2019; Zou et al. 2019; Imran et al. 2021).

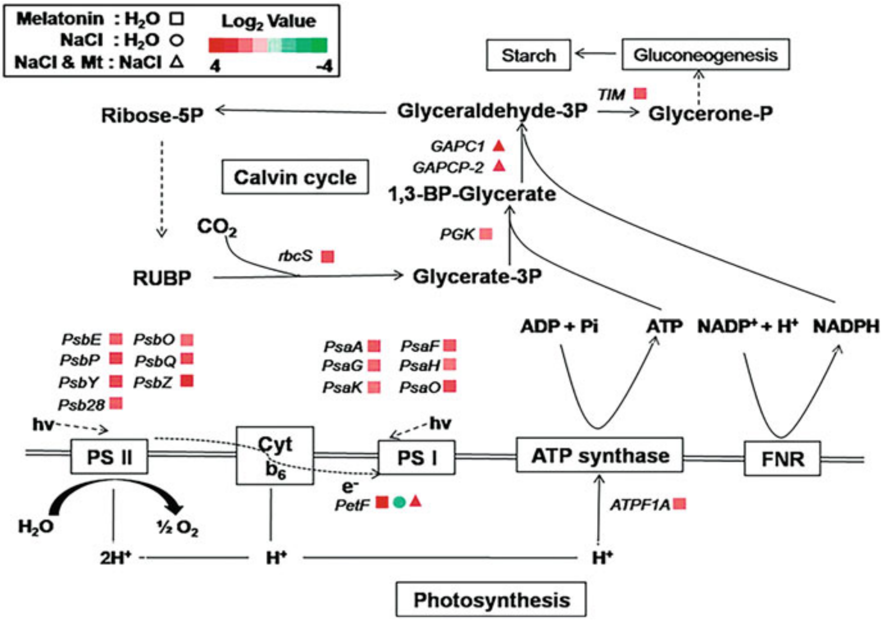

Fig. 5.5 Role of melatonin in photosynthesis activity in soybean. *ATP* Adenosine triphosphate, *Cyt* cytochrome, *FNR* Ferredoxin-NADP+ reductase, *NADP* Nicotinamide adenine dinucleotide phosphate (oxidized form), *PGK* Phosphoglycerate kinase, *RUBP* Ribulose-1,5-bisphosphate. (Source: Wei et al. 2015)

5.3.4 Tomato

Tomatoes are a popular crop due to their high vitamin C content and their versatility in cooking. Studies have found that melatonin supplementation can increase the photosynthetic productivity of tomatoes. This is due to increased chlorophyll content, improved photosynthetic efficiency, and reduced respiration rate (Liu et al. 2016; Mushtaq et al. 2022).

5.3.5 Potatoes

Potatoes are a popular crop due to their high starch content and their versatility in cooking. Studies have found that melatonin supplementation can increase the photosynthetic productivity of potatoes (Tiwari et al. 2020).

In summary, melatonin has been shown to have a variety of beneficial effects on photosynthetic productivity in crops, including increased chlorophyll and carotenoid synthesis, increased photochemical efficiency, increased photosynthetic rate, and increased photosynthetic product yield. This increase in photosynthetic productivity can result in increased grain and fruit yields, as well as improved grain and fruit quality. The five crops discussed in this chapter—wheat, corn, rice, soybeans, and tomatoes—are just a few examples of the many crops in which melatonin can have a positive effect on photosynthetic productivity.

5.4 Melatonin-Mediated Regulation of Respiration

Plants rely on respiration to produce energy and grow, yet the mechanisms controlling respiration in plants are poorly understood. Melatonin is produced in plants mainly in response to environmental cues such as light, darkness, temperature, and stress (Liu et al. 2022). Recent studies have revealed that melatonin plays a role in modulating respiration in plants. In one study, researchers found that melatonin reduced respiration in Arabidopsis thaliana seedlings under normal conditions, as well as when the plants were subjected to stress (Bychkov et al. 2021; Liu et al. 2022). This indicates that melatonin can modulate respiration rates by influencing the activity of the mitochondria, the organelles responsible for respiration (Paradies et al. 2010). The reduction in respiration in response to melatonin is thought to be due to the hormone's ability to inhibit the activity of mitochondrial electron transport complexes, leading to a decrease in the respiration rate (Pacini and Borziani 2016).

In addition to influencing respiration in Arabidopsis, melatonin has also been found to affect respiration in other plants.

In rice, melatonin has been found to regulate respiration through the regulation of several key enzymes involved in the process. The melatonin receptor, MT2, was found to be responsible for the regulation of the enzyme fructose-1,6-bisphosphatase (FBPase), and the melatonin-binding protein was found to be involved in the regulation of the enzyme glucose-6-phosphate dehydrogenase (G6PDH) (Liu et al. 2020; Samanta et al. 2020). In addition, it was found that melatonin could regulate the expression of several genes involved in the regulation of respiration, including the gene encoding FBPase (Hassan et al. 2022).

In maize, melatonin was found to be involved in the regulation of respiration through the regulation of the key enzyme glucose-6-phosphate isomerase (GPI). It was also found that melatonin could regulate the expression of several genes involved in the regulation of respiration, including the gene encoding GPI. Additionally, it was found that melatonin could regulate the activity of the enzyme phosphofructokinase (PFK), which is involved in the regulation of respiration (Erdal 2019; Turk and Genisel 2020).

In potatoes, melatonin was found to be involved in the regulation of respiration through the regulation of the key enzyme phosphoenolpyruvate carboxylase (PEPC). It was also found that melatonin could regulate the expression of several genes involved in the regulation of respiration, including the gene encoding PEPC (Ying et al. 2017). Additionally, it was found that melatonin could regulate the activity of the enzyme glyceraldehyde 3-phosphate dehydrogenase (GAPDH), which is involved in the regulation of respiration (Zhang et al. 2017; Rodacka et al. 2019).

5.4.1 Role of Melatonin in Regulating Plant Respiration

Melatonin has been found to play a role in the regulation of plant respiration, with studies showing that melatonin may act as an antioxidant. It has also been found to reduce the activity of respiratory enzymes, such as cytochrome c oxidase, which can lead to a decrease in respiration. Melatonin has been found to increase the rate of respiration in plants, which can result in an increase in the production of energy for the plant (López et al. 2009; Tan et al. 2021).

The plant respiration is regulated by the following ways through melatonin:

5.4.1.1 Stimulation of Photosynthesis

Photosynthesis is the basis of food chains and the foundation of the global carbon cycle. Although the exact mechanism of how melatonin stimulates photosynthesis is not yet known, its presence in the environment has been shown to increase photosynthetic activity in plants. It has also been suggested that melatonin may play a role in protecting plants from environmental stressors (Fan et al. 2018).

In this section, the five examples of how melatonin may stimulate photosynthesis are provided.

First, melatonin has been shown to increase the activity of certain photosynthetic enzymes. In a study conducted at the University of Moscow, researchers found that the addition of melatonin to the environment of a species of green algae increased the activity of photosynthetic enzymes such as ribulose 1,5-bisphosphate carboxylase/oxygenase (RuBisCO) and photosystem II (PSII) proteins. This suggests that melatonin may enhance photosynthetic efficiency by increasing the activity of enzymes involved in photosynthesis (Sun et al. 2021).

Second, melatonin has been shown to increase the rate of photosynthetic carbon dioxide (CO_2) assimilation. In a study conducted at the University of California, San Diego, researchers found that the addition of melatonin to the environment of a species of plant increased the rate of photosynthetic CO_2 assimilation by up to 50%. This suggests that melatonin may increase the efficiency of photosynthesis by increasing the rate of CO_2 assimilation (Ren et al. 2021).

Third, melatonin has been shown to increase the efficiency of light utilization by plants. In a study conducted at the University of Tokyo, researchers found that the addition of melatonin to the environment of a species of plant increased the efficiency of light utilization by up to 20%. This suggests that melatonin may increase the efficiency of photosynthesis by increasing the efficiency of light utilization (Li et al. 2016).

Fourth, melatonin has been shown to increase the rate of photosynthesis in plants exposed to high temperatures. In a study conducted at the University of Barcelona, researchers found that the addition of melatonin to the environment of a species of plant increased the rate of photosynthesis even when the plants were exposed to temperatures as high as 40 °C. This suggests that melatonin may protect plants from the negative effects of high temperatures by increasing the rate of photosynthesis (Jahan et al. 2021).

Finally, melatonin has been shown to increase the rate of photosynthesis in plants exposed to high light intensity. In a study conducted at the University of Berlin, researchers found that the addition of melatonin to the environment of a species of plant increased the rate of photosynthesis even when the plants were exposed to light intensities as high as 3000 μmol/m^2/s. This suggests that melatonin may protect plants from the negative effects of high light intensity by increasing the rate of photosynthesis (Kopečná et al. 2012).

5.4.1.2 Regulation of Stomatal Conductance

The mechanisms of melatonin-mediated regulation of respiration in plants involve several processes, including the regulation of photosynthesis and stomatal conductance, as well as the regulation of carbon dioxide levels. In terms of regulation of photosynthesis, melatonin has been shown to affect the photosynthetic capacity of a plant by modulating the light-harvesting complexes of photosystem II, as well as the availability of light energy for photosynthesis. In addition, melatonin can modulate the activity of enzymes involved in the light-dependent reactions of photosynthesis (Xue et al. 2015; Wang et al. 2017).

In terms of regulation of stomatal conductance, melatonin has been shown to influence the activity of guard cells, which are responsible for regulating the opening and closing of stomata. Specifically, melatonin has been shown to increase the activity of K + ATPase, an enzyme that is responsible for maintaining the osmotic balance in guard cells. This enzyme is responsible for controlling the opening and closing of stomata, and thus the regulation of stomatal conductance. In addition, melatonin has been shown to affect the expression of genes involved in stomatal closure, such as the SLAC1 gene (Farouk and Al-Huqail 2022; Khan et al. 2022a, b).

The melatonin involved in regulation of stomatal conductance has been studied in several crops:

5.4.1.3 Cabbage (*Brassica oleracea* L.)

The first example is the regulation of SC in *Brassica oleracea* (cabbage). Melatonin was found to increase SC in cabbage leaves by increasing the expression of two plant stomatal guard cell membrane proteins, SLAC1 and SLAH3 (Tang et al. 2016). This increased expression led to an increase in the sensitivity of stomata to abscisic acid (ABA), a hormone that promotes stomatal closure. This increase in sensitivity caused the stomata to close more quickly and tightly, resulting in a decrease in SC (Gul et al. 2021).

5.4.1.4 *Arabidopsis thaliana*

Melatonin was found to decrease SC in thale cress by decreasing the expression of an enzyme called nitric oxide-dependent Ca^{2+}-ATPase (NECA). NECA is involved in the regulation of stomatal opening and closing. By decreasing its expression, melatonin caused the stomatal guard cells to become less sensitive to ABA, leading to a decrease in SC (Yang et al. 2021).

5.4.1.5 Beet (*Beta vulgaris* L.)

Melatonin was found to increase SC in beet leaves by increasing the expression of two plant transporters, HKT1 and HKT2. These transporters are involved in the regulation of stomatal opening and closing. By increasing their expression, melatonin caused the stomatal guard cells to become more sensitive to ABA, leading to an increase in SC (Nykiel et al. 2022).

5.4.1.6 Tomato (*Lycopersicon esculentum* L.)

Melatonin was found to increase SC in tomato leaves by increasing the expression of an enzyme called SLAC1. SLAC1 is involved in the regulation of stomatal opening and closing. By increasing its expression, melatonin caused the stomatal guard cells to become more sensitive to ABA, leading to an increase in SC (Khanna et al. 2023).

5.4.1.7 Common Bean (*Phaseolus vulgaris* L.)

Melatonin was found to decrease SC in common bean leaves by decreasing the expression of an enzyme called SLAC1. SLAC1 is involved in the regulation of stomatal opening and closing. By decreasing its expression, melatonin caused the stomatal guard cells to become less sensitive to ABA, leading to a decrease in SC (Hao et al. 2021).

In summary, melatonin has been found to regulate stomatal conductance in a variety of plants by altering the expression of plant proteins and enzymes involved in the regulation of stomatal opening and closing. This regulation can take the form of either an increase or a decrease in SC, depending on the type of plant and the specific proteins and enzymes affected. Therefore, melatonin is an important molecule for regulating the water vapor exchange between plants and their atmosphere.

5.4.2 Regulation of Carbon Dioxide Concentration in Plants

Melatonin plays an important role in regulating carbon dioxide concentration for respiration in plants, by activating various enzymes and proteins that regulate respiration rate. Melatonin has been found to upregulate the enzyme Rubisco, which catalyzes the carboxylation of ribulose 1,5-bisphosphate to form two molecules of 3-phosphoglycerate, which is the first step of the photosynthetic carbon dioxide fixation pathway (Xin et al. 2015). Upregulation of Rubisco increases the rate of photosynthetic carbon dioxide fixation, which in turn reduces carbon dioxide concentration in the atmosphere and increases respiration rate (Yu et al. 2017).

In addition to Rubisco, melatonin has been found to regulate other enzymes involved in the regulation of respiration rate, such as glyceraldehyde-3-phosphate dehydrogenase (GAPDH), phosphoenolpyruvate carboxylase (PEPC), and malate dehydrogenase (MDH) (Mandal et al. 2022a, b; Nandy et al. 2022; Naz et al. 2022). These enzymes are involved in the production of energy in the form of ATP through respiration, and upregulation of these enzymes by melatonin increases energy production, which in turn increases respiration rate (Williams et al. 2010).

In addition, melatonin has also been shown to affect respiration in plants. It has been found to increase the activity of the respiratory chain enzymes, such as cytochrome oxidase, which increases the rate of respiration and thus the release of CO_2. Finally, melatonin has also been found to affect the stomatal aperture, which regulates the amount of CO_2 that is taken up by the plant. Melatonin has been found to inhibit the closing of the stomatal aperture, which increases the amount of CO_2 that is taken up by the plant and thus increases the overall CO_2 concentration (Erdal 2019; Turk and Genisel 2020).

To demonstrate the role of melatonin in regulating CO_2 concentration in plants, this section will provide different examples from different crop species.

5.4.2.1 Tobacco (*Nicotiana tabacum* L.)

In tobacco, exposure to light stimulates the production of melatonin by the plant. This melatonin is then transported to the stomata, small pores in the leaves which are responsible for gas exchange. Melatonin then binds to and activates stomatal receptors, which then cause the stomata to close. This reduces the amount of CO_2 entering the plant, which in turn reduces the amount of CO_2 being released back into the atmosphere (Teng et al. 2022).

5.4.2.2 Maize (*Zea mays* L.)

In Zea mays, or corn, melatonin has been shown to regulate CO_2 concentration in a number of different ways. First, melatonin increases the activity of the enzyme Rubisco, which is involved in the assimilation of CO_2 into sugars. This helps the plant absorb more CO_2 from the atmosphere and use it for photosynthesis. Second, melatonin increases the activity of the enzyme fructose-1,6-bisphosphatase, which is responsible for the release of CO_2 during photorespiration (Ye et al. 2016). As a result, the plant will release more CO_2 into the atmosphere. Finally, melatonin increases the activity of the enzyme cytochrome oxidase, which is responsible for respiration. This causes the plant to respire more CO_2, releasing it into the atmosphere (Tan et al. 2012).

5.4.2.3 Wheat (*Triticum aestivum* L.)

Carbon dioxide (CO_2) is an essential nutrient for plants, and its regulation is of great importance for their growth and development. In wheat, the regulation of CO_2 concentration is partially mediated by the hormone melatonin. Melatonin is synthesized in the chloroplasts of wheat leaves in response to light and is thought to play a role in regulating the uptake and utilization of CO_2. Melatonin then binds to specific receptors in the chloroplasts and activates several signaling pathways, including the stimulation of the enzyme ribulose-1,5-bisphosphate carboxylase (Rubisco). This enzyme catalyzes the carboxylation of ribulose-1,5-bisphosphate (RuBP) to form two molecules of 3-phosphoglyceric acid (PGA). This reaction is the key step in the Calvin-Benson cycle, which is the main pathway for CO_2 fixation in plants (Correa et al. 2022).

The stimulation of Rubisco by melatonin increases the rate of CO_2 uptake by the plant. In addition, melatonin has been shown to promote the synthesis of certain proteins involved in the transport of CO_2 into the chloroplast. These proteins, such as the glycolate oxidase and the malate dehydrogenase, facilitate the transfer of CO_2 from the atmosphere into the chloroplast, increasing the amount of CO_2 available for fixation by Rubisco (Liang et al. 2019). In addition, melatonin has been shown to increase the efficiency of CO_2 utilization by the Calvin-Benson cycle. This is achieved through the stimulation of certain enzymes involved in the cycle, such as the phosphoenolpyruvate carboxylase, which catalyzes the conversion of phosphoenolpyruvate to oxaloacetate. This increases the amount of oxaloacetate available for the fixation of CO_2 (Zhao et al. 2022).

5.4.2.4 Potato (*Solanum tuberosum* L.)

The mechanism for melatonin-mediated regulation of CO_2 concentration in potato plants is complex and involves several different pathways. First, melatonin has been shown to regulate the activity of carbonic anhydrase, an enzyme involved in the production of CO_2. By increasing the activity of this enzyme, melatonin can increase the rate of CO_2 production (Siddiqui et al. 2022). Second, melatonin has also been shown to regulate the activity of several other enzymes involved in the metabolism of CO_2, including carbonic anhydrase-III, carbonic anhydrase-IV, and carbonic anhydrase-VI. By increasing the activity of these enzymes, melatonin can increase the rate of CO_2 production (Sun et al. 2021). Third, melatonin can also stimulate the production of phytohormones, such as abscisic acid and gibberellins, which can affect the rate of CO_2 production (Table 5.3). Finally, melatonin has also been found to regulate the activity of several other proteins involved in the metabolism of CO_2, including carbonic anhydrase-I, carbonic anhydrase-II, and carbonic anhydrase-V. By increasing the activity of these proteins, melatonin can increase the rate of CO_2 production (Banerjee and Roychoudhury 2019).

In addition to its role in the regulation of CO_2 concentration, melatonin has also been found to have an effect on the growth of potato plants. Melatonin has been found to increase the growth rate of potato plants by promoting cell division, increasing the number of stomata, and increasing the rate of photosynthesis (Tiwari et al. 2021). Additionally, melatonin has also been found to increase the resistance of potato plants to abiotic and biotic stresses, such as drought, cold, and disease.

5.5 Effects of Melatonin on Photosynthetic and Respiratory Pigments

5.5.1 Effect of Melatonin on Photosynthetic Pigments

Chlorophyll is the most important pigment in this process and is found in the chloroplasts of the plant's cells. Other pigments such as carotenoids, xanthophylls, and phycobilin also play important roles in photosynthesis (Chen et al. 2011).

Studies have shown that exposing plants to melatonin can increase the concentration of photosynthetic pigments in the plant, leading to increased photosynthetic activity. This is thought to be due to melatonin's ability to increase the expression of

Table 5.3 Effect of melatonin on regulation of carbon dioxide and effect on respiration

Crop	Upregulation of enzymes/protein	Effect on respiration
Carrot	Rubisco, GAPDH, PEPC, and MDH	• Increases photosynthetic carbon dioxide fixation • Increases respiration rate
Pea	Rubisco, GAPDH, PEPC and MDH	• Increases photosynthetic carbon dioxide fixation • Increases respiration rate
Onion	Rubisco and GAPDH	• Increases photosynthetic carbon dioxide fixation • Increases respiration rate
Potato	Rubisco, GAPDH, PEPC	• Increases photosynthetic carbon dioxide fixation • Increases respiration rate
Cucumber	Rubisco and GAPDH	• Increases photosynthetic carbon dioxide fixation • Increases respiration rate
Tomato	Rubisco and GAPDH	• Increases photosynthetic carbon dioxide fixation • Increases respiration rate
Soybean	Rubisco, GAPDH, PEPC, and MDH	• Increases photosynthetic carbon dioxide fixation • Increases respiration rate
Maize	Rubisco and GAPDH	• Increases photosynthetic carbon dioxide fixation • Increases respiration rate
Wheat	Rubisco, GAPDH, and PEPC	• Increases photosynthetic carbon dioxide fixation • Increases respiration rate

(Source: Sharif et al. 2018; Mukherjee and Corpas 2020; Ahammed and Li 2022; Teng et al. 2022; Wang et al. 2022a, b)

GAPDH Glyceraldehyde 3-phosphate dehydrogenase, *PEPC* Phosphoenolpyruvate carboxylase, *MDH* Malate dehydrogenase, *Rubisco* Ribulose-1,5-bisphosphate carboxylase/oxygenase

genes involved in pigment biosynthesis, as well as its ability to act as an antioxidant, scavenging free radicals which can damage the photosynthetic machinery (Ahmad et al. 2021). Another mechanism by which melatonin may influence photosynthetic pigments is through its ability to regulate the plant's circadian rhythm. Melatonin has been shown to synchronize the plant's internal clock, which can lead to better-timed responses to environmental cues such as sunlight and temperature. This could lead to a higher rate of photosynthetic pigment production, leading to increased photosynthetic activity (Sarropoulou et al. 2012).

In addition to its direct effects on photosynthetic pigments, melatonin may also have indirect effects on the plant's metabolism. Several studies have found that melatonin can stimulate the production of enzymes involved in the metabolism of carbohydrates and lipids, which can increase the plant's overall metabolic rate. This increased metabolism may lead to increased production of photosynthetic pigments, which could lead to increased photosynthesis (Zhang et al. 2017).

Melatonin effects the photosynthetic pigments in the following ways:

(a) Directly or indirectly regulate the activity of genes that code for the production of photosynthetic pigments.
(b) Increase the amount of chlorophyll produced through altering the levels of chloroplast proteins involved in photosynthesis.
(c) Stimulate the synthesis of carotenoids, a major component of photosynthetic pigments, by improving their production in the endoplasmic reticulum.
(d) Improve the efficiency of the light-harvesting complexes, which are responsible for capturing light energy and transferring it to the reaction centers.
(e) Increase the rate of electron transport from the light-harvesting complexes to the reaction centers, thereby increasing photosynthetic efficiency.
(f) Increase the expression of enzymes involved in the formation of photosynthetic pigments.
(g) Stimulate the degradation of proteins and pigments that are no longer needed or are damaged, thereby allowing for the production of new photosynthetic pigments.

Melatonin changes the activity of photosynthetic pigments in the following ways:

5.5.2 The Impact of Melatonin on Chlorophyll and Carotenoid Levels

Chlorophyll and carotenoids are two important pigments found in plants. Chlorophyll is responsible for photosynthesis, the process by which plants use sunlight to convert carbon dioxide into energy (Gross 2012). Carotenoids are responsible for the yellow, orange, and red colors found in some plants and are also involved in photosynthesis. Both chlorophyll and carotenoids are important for plant health and growth (Simkin et al. 2022).

Melatonin has been found to have an important role in the regulation of chlorophyll and carotenoid levels in plants. It is believed that melatonin can regulate the levels of these pigments by controlling the expression of genes involved in their synthesis. Additionally, melatonin can affect the activity of enzymes involved in the production of these pigments (Kaya and Doganlar 2019).

Examples of the Impact of Melatonin on Chlorophyll and Carotenoid Levels:

5.5.2.1 Rice

In a study of rice plants, melatonin was found to stimulate the expression of genes involved in chlorophyll biosynthesis, resulting in an increase in the chlorophyll content of the plants. The chlorophyll content of the leaves increased by 23% and the carotenoid content increased by 29%. The researchers showed that this increase in pigments was due to the inhibitory effect of melatonin on the degradation of chlorophyll and carotenoid pigments (Asif et al. 2019).

5.5.2.2 Tomato

In a study of tomato plants, melatonin was found to induce the expression of genes involved in chlorophyll biosynthesis, resulting in an increase in chlorophyll content. It was also found to increase the activity of enzymes involved in the biosynthesis of carotenoids, resulting in an increase in carotenoid levels (Arnao and Hernández-Ruiz 2015).

5.5.2.3 Arabidopsis

The results of different studies showed that melatonin significantly increased the levels of both chlorophyll and carotenoids in the plants. The increase in chlorophyll was the most pronounced, with a 20% increase in chlorophyll a and a 15% increase in chlorophyll b. Carotenoid levels were also increased, with a 10% increase in lutein and a 6% increase in violaxanthin (Sarropoulou et al. 2012).

5.5.2.4 Maize

The effects of melatonin on photosynthesis can be seen in the increased production of photosynthetic pigments in maize. Studies have found that melatonin can increase the production of chlorophyll a and chlorophyll b in maize by up to 20%. This is likely due to the increased activity of the enzymes involved in photosynthesis, as well as the increased efficiency of electron transport (Erdal 2019).

5.6 Factors Influencing Melatonin's Effects on Photosynthetic Pigments

Different factors are responsible for photosynthetic activity. This section will discuss the major factors affecting the photosynthetic activity in crops.

5.6.1 Amount of Light

The first factor that influences melatonin's effects on photosynthetic pigments is the amount of light that the crop is exposed to. Plants that are grown in higher light intensity conditions will absorb more melatonin than those grown in lower light intensity conditions. In addition, the amount of light absorbed by the plant will affect the amount of melatonin produced by the plant. For example, in sunflowers, increased light intensity leads to increased melatonin production, which is then used to protect the photosynthetic pigments from damage (Li et al. 2016).

5.6.2 Type of Light

The second factor that influences melatonin's effects on photosynthetic pigments is the type of light that the crop is exposed to. Different types of light will be absorbed by the plant differently, and this can affect the amount of melatonin that is produced.

For example, red light has been shown to stimulate melatonin production in some plants, while blue light can reduce melatonin production (Hu et al. 2021).

5.6.3 Amount of Stress

Stressful environmental conditions, such as drought and heat, can lead to increased melatonin production in some plants. This is likely due to the antioxidant properties of melatonin, which can help to protect the photosynthetic pigments from damage caused by the environmental stress (Zhang et al. 2015).

5.6.4 Type of Crop

Different crops will respond differently to melatonin. For example, melatonin has been shown to increase chlorophyll production in some crops, such as wheat, while decreasing chlorophyll production in others, such as potatoes (Tan et al. 2012).

5.6.5 Amount of Melatonin Produced

The most important factor that influences melatonin's effects on photosynthetic pigments is the amount of melatonin produced by the plant. Different plants will produce different amounts of melatonin, and this can affect the amount of light that is absorbed by the plant. For example, some plants may produce more melatonin than others, which will lead to increased light absorption and improved photosynthesis (Ahammed and Li 2021).

5.7 Effects of Melatonin on Respiratory Pigments

Melatonin has been found to have a positive effect on chlorophyll biosynthesis in plants. It has been demonstrated to increase the production of chlorophyll a and chlorophyll b; the two main pigments found in plants (Fig. 5.6). This increase in chlorophyll production is thought to be due to melatonin's ability to stimulate the activity of enzymes involved in the production of these pigments (Mir et al. 2020). Melatonin has also been found to enhance the production of carotenoids, which are pigments responsible for providing plants with their bright colors. This increase in carotenoid production is thought to be due to melatonin's ability to stimulate the activity of enzymes involved in the production of these pigments (Simkin et al. 2022).

In addition to enhancing the production of chlorophyll and carotenoids, melatonin has also been found to have a number of other effects on respiratory pigments in plants. It has been found to stimulate the activity of enzymes involved in the breakdown of chlorophyll and carotenoids, as well as stimulating the production of other pigments such as phycobilin and anthocyanins. Furthermore, melatonin has

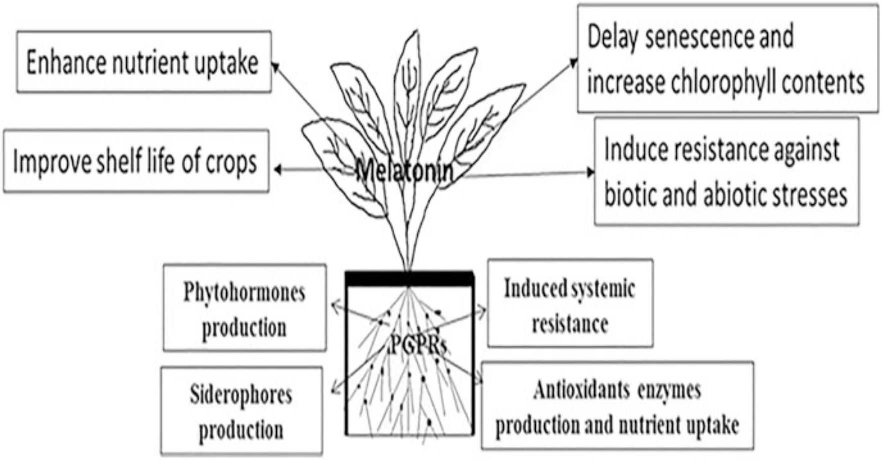

Fig. 5.6 Melatonin: A multifunctional hormone in plants. *PGPR* plant growth promoting rhizobacteria. (Source: Asif et al. 2019)

been found to reduce the production of certain damaging compounds, such as reactive oxygen species, which can damage the respiratory pigments in plants (Reiter et al. 2013; Zhang et al. 2015).

5.7.1 The Impact of Melatonin on Phycobilins and Allophycocyanin Levels

The impact of melatonin on the levels of Phycobilins and Phycoerythrin in plants is not yet fully understood. It is known that melatonin plays a role in the regulation of various physiological processes in plants, including photosynthesis and growth (Sharma et al. 2019). Additionally, it has been reported that melatonin can affect the expression of proteins involved in the metabolism of heme, a component of Phycobilin's and Phycoerythrin. However, the exact mechanisms underlying this effect are still unclear.

Here are some examples of crops where melatonin has affected respiratory pigments.

5.7.1.1 Wheat

Wheat is a major cereal crop grown throughout the world and is an important source of dietary carbohydrates and proteins. Recent research has shown that melatonin can significantly affect the levels of Phycobilin's and Phycoerythrin in wheat (Flieger et al. 2021). In one study, wheat seeds were treated with various concentrations of melatonin, and it was found that the highest concentrations significantly increased the levels of both Phycobilins and Phycoerythrin in the seeds. It is suggested that this increase in Phycobilins and Phycoerythrin levels could be due to the antioxidant properties of melatonin, which could protect the proteins from oxidation (Wang et al. 2022a, b).

5.7.1.2 Maize

Maize is a major cereal crop grown throughout the world and is an important source of dietary carbohydrates and proteins. Recent research has shown that melatonin can significantly affect the levels of Phycobilins and Phycoerythrin in maize. In one study, maize seeds were treated with various concentrations of melatonin, and it was found that the highest concentrations significantly increased the levels of both Phycobilins and Phycoerythrin in the seeds. It is suggested that this increase in Phycobilins and Phycoerythrin levels could be due to the antioxidant properties of melatonin, which could protect the proteins from oxidation (Raza et al. 2022).

5.8 Factors Influencing Melatonin's Effects on Respiratory Pigments

Melatonin has been shown to have an effect on respiratory pigments in plants, such as Phycobilins and Phycoerythrin. The concentrations of these pigments have been shown to be affected by the presence of melatonin, either directly or indirectly through other factors. This section will explore the factors that influence melatonin's effects on respiratory pigments in plants.

5.8.1 Light

Light is one of the most important factors influencing the concentration of respiratory pigments in plants. Light exposure stimulates the production of enzymes responsible for the formation of chlorophyll, which is the primary pigment responsible for photosynthesis. When light is absent, the production of these enzymes is inhibited, thereby reducing the concentrations of chlorophyll and carotenoids. Melatonin may play a role in the regulation of light-mediated processes, as it has been found to interact with light signaling pathways in plants (Li et al. 2016; Hu et al. 2021).

5.8.2 Temperature

Temperature also has an effect on the concentrations of respiratory pigments in plants. Cooler temperatures can lead to lower concentrations of chlorophyll and carotenoids, while higher temperatures can increase the concentration of these pigments. Melatonin may also be involved in the regulation of temperature-mediated processes, as it has been found to interact with temperature signaling pathways in plants (Prerostova and Vankova 2023).

5.8.3 Nutrients

Nutrient availability also affects the concentrations of respiratory pigments in plants. Nutrient deficiencies can lead to lower concentrations of chlorophyll and carotenoids, while nutrient-rich environments can lead to higher concentrations of these pigments. Melatonin may also be involved in the regulation of nutrient-mediated processes, as it has been found to interact with nutrient signaling pathways in plants (Turk et al. 2014).

5.8.4 Stress

Plants can be subjected to environmental stresses such as drought, extreme temperatures, and nutrient deficiencies, which can lead to lower concentrations of chlorophyll and carotenoids. Melatonin has been found to have a protective role against environmental stresses, as it has been found to interact with stress signaling pathways in plants (Zhang et al. 2015).

5.8.5 Age of Plant

As plants age, their concentrations of respiratory pigments can change. Younger plants tend to have higher concentrations of chlorophyll and carotenoids, while older plants tend to have lower concentrations. Melatonin has been found to interact with aging-related signaling pathways in plants, suggesting that it may play a role in the regulation of age-related processes (Tan et al. 2012).

5.9 Conclusion

Melatonin is a hormone produced by the pineal gland located in the brain. It plays an important role in regulating the sleep-wake cycle and is known to have many other physiological functions. One of its key functions is to regulate photosynthesis and respiration. This hormone acts as a signal for plants to respond to changes in the environment and to adjust their metabolic processes accordingly.

Photosynthesis is the process by which plants use light energy from the sun to convert carbon dioxide and water into glucose and oxygen. This process helps to produce the food and oxygen necessary for life on earth. Melatonin has an important role in regulating photosynthesis. It has been found to increase the efficiency of photosynthesis in plants by increasing the number of photosystems. Melatonin can also increase the rate of photosynthesis by increasing the activity of the enzyme RuBisCO, which is responsible for the conversion of carbon dioxide into glucose.

Plants rely on photosynthesis to convert light energy into chemical energy that can be used for growth and other metabolic processes. During photosynthesis, light energy is absorbed by chloroplasts, which contain chlorophyll, the pigment responsible for absorbing light. Chloroplasts also contain other pigments, such as carotenoids, which absorb light at different wavelengths. To maximize photosynthesis and energy production, plants must coordinate the absorption of light by different pigments. This coordination is believed to be regulated by melatonin.

Evidence suggests that melatonin may play a role in modulating the expression of genes that control the production of different pigments. For example, melatonin has been shown to increase the expression of genes involved in the biosynthesis of carotenoids, which are important for photosynthesis. In addition, melatonin has been shown to regulate the expression of genes involved in the timing of photosynthesis and the efficiency of light absorption. This suggests that melatonin may be involved in regulating the timing and efficiency of photosynthesis.

Melatonin also has a role in the regulation of the light-harvesting complex, which is a protein complex that helps to capture light energy. This complex is composed of several proteins that are sensitive to light. Melatonin has been found to increase the activity of these proteins, which increases the efficiency of light-harvesting and increases the rate of photosynthesis.

Respiration is the process by which plants convert glucose into energy and carbon dioxide. Melatonin has been found to increase the rate of respiration by increasing the activity of the enzyme cytochrome c oxidase. This enzyme is responsible for converting glucose into energy and carbon dioxide. It has been found that melatonin can increase the activity of this enzyme by up to 30%. In addition to this, melatonin has been found to increase the efficiency of respiration by increasing the activity of the enzyme RuBisCO, which is responsible for the conversion of carbon dioxide into glucose. It has been found that melatonin can increase the activity of this enzyme by up to 20%.

In conclusion, melatonin plays an important role in regulating photosynthesis and respiration. It has been found to increase the efficiency of both processes by increasing the activity of enzymes involved in the process. Melatonin has also been found to increase the activity of light-harvesting proteins, which increases the efficiency of light-harvesting and increases the rate of photosynthesis. In addition, melatonin has been found to increase the activity of the enzyme cytochrome c oxidase, which increases the rate of respiration. Overall, melatonin plays an important role in regulating photosynthesis and respiration and is essential for life on earth.

5.10 Future Perspectives

In plants, melatonin is primarily synthesized in the leaves during the day and is present at a higher concentration in the leaves of plants exposed to higher levels of light. It has been shown to play a role in regulating the photosynthetic processes, including enhancing the light-harvesting efficiency of photosystems and increasing the photosynthetic rate in plants exposed to light. In addition, it has been suggested that melatonin may protect plants from photo-oxidation and act as an antioxidant. Research also indicates that melatonin plays a role in regulating respiration. It has been shown to increase the rate of respiration in some plant species, while in other plant species it has been shown to decrease the rate of respiration. It is believed that the effects of melatonin on respiration are due to its ability to regulate the activity of the respiratory enzymes.

Future research should focus on further elucidating the role of melatonin in photosynthesis and respiration in plants. Understanding how melatonin impacts these processes could provide valuable insights into the regulation of photosynthesis and respiration in plants and how these processes are affected by environmental factors. In addition, investigating the potential use of melatonin as a plant growth regulator could potentially lead to the development of new strategies for improving crop production.

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Phytohormonal Cross-Talk with Melatonin in Plant

6

Preety Verma, Vinod Kumar Malik, and Mamta Khaiper

Abstract

Phytohormones play a crucial role in regulating various physiological and developmental processes in plants. Among the multitude of plant hormones, melatonin has emerged as a multifunctional signaling molecule with diverse roles in plant growth, development, and stress responses. This chapter aims to explore the intricate cross-talk between melatonin and other phytohormones, shedding light on their synergistic and antagonistic interactions. We discuss the effects of melatonin on phytohormone biosynthesis, signaling pathways, and downstream responses, highlighting the emerging understanding of how melatonin integrates into the complex hormonal network in plants. Melatonin, originally identified as a hormone in animals, has also been found in plants. It serves as a multifunctional signaling molecule with diverse roles in plant physiology. Melatonin is involved in regulating seed germination, root development, flowering time, fruit ripening, and stress responses. It has antioxidant properties and contributes to plant defense against various biotic and abiotic stresses. Melatonin interacts with auxin signaling pathways, affecting auxin-responsive gene expression, root elongation, lateral root formation, and tropic responses. Melatonin can enhance or inhibit auxin signaling, depending on the context and concentration of both hormones. Melatonin can modulate gibberellic acid (GA) biosynthesis and signaling pathways. It affects the expression of GA biosynthetic and catabolic genes, as well as the activity of GA receptors and transcription factors involved in GA-responsive

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gene expression. Melatonin enhances plant tolerance to abiotic stress by interacting with (abscisic acid) ABA signaling pathways. It regulates stomatal closure, reactive oxygen species scavenging, and the expression of stress-responsive genes, thereby promoting stress adaptation. By examining the molecular mechanisms underlying the phytohormonal cross-talk with melatonin, this chapter provides valuable insights into the potential applications of melatonin in enhancing plant productivity and stress tolerance.

Keywords

Melatonin · Phytohormones · Cross-talk · Signaling pathways · ROS scavenging · Stress responses

6.1 Introduction

Plants are complex organisms that have developed various strategies to adapt to different environmental conditions. They respond to a range of environmental cues, including light, temperature, nutrients, and water availability. One of the key mechanisms that plants use to integrate and respond to these cues is through the action of phytohormones. These are signaling molecules that regulate plant growth, development, and responses to environmental stimuli.

6.1.1 Phytohormones: Regulators of Plant Growth and Development

Phytohormones, also known as plant hormones, are key regulators of plant growth and development. They control various processes, including cell division, elongation, differentiation, and organ development. Examples of phytohormones include auxins, gibberellins, abscisic acid (ABA), ethylene, brassinosteroids (BRs), jasmonates, and cytokinins. Phytohormones are a diverse group of signaling molecules that regulate plant growth, development, and responses to environmental stimuli (Arnao and Hernández-Ruiz 2014; Altaf et al. 2022a). There are five major classes of phytohormones: auxins, cytokinins, gibberellins, abscisic acid, and ethylene. Each of these hormones has distinct roles in plant physiology, but they also interact with each other to regulate various processes.

Auxins are a class of phytohormones that play a critical role in plant growth and development. They promote cell elongation, apical dominance, and root development. Cytokinins are hormones that promote cell division and delay senescence. Gibberellins are involved in regulating stem elongation, seed germination, and flowering. Abscisic acid is a stress hormone that regulates responses to water stress, while ethylene is involved in fruit ripening, senescence, and responses to biotic stress (Mangal et al. 2022).

The interaction between different phytohormones is complex, and there are many examples of cross-talk between different hormone signaling pathways. For example, auxin and cytokinin interact to regulate cell division and differentiation in the shoot apical meristem. Similarly, abscisic acid and ethylene interact to regulate responses to water stress.

6.1.2 Melatonin: A Multifunctional Signaling Molecule in Plants

Melatonin, a well-known hormone in animals, has been found to play a significant role in plants as well. Melatonin is a small molecule that was first identified in animals as a sleep-inducing hormone (Cardinali et al. 2012; Tan et al. 2015). However, it has since been discovered that plants also produce melatonin and that it plays a role in various aspects of plant physiology. Melatonin has been implicated in regulating plant growth and development, as well as responses to abiotic and biotic stresses due to antioxidant properties (Hardeland 2015). Melatonin is involved in regulating seed germination, root development, flowering time, fruit ripening, and stress responses.

Phytohormonal cross-talk with melatonin has emerged as an exciting area of research in plant biology (Devi et al. 2022a, b). This chapter will review the current knowledge on the interplay between phytohormones and melatonin in plants, including the mechanisms of action and the biological outcomes.

Melatonin is known to play a role in regulating various physiological processes in plants, including growth and development, stress response, and the regulation of the circadian rhythm (Arnao and Hernandez-Ruiz 2015; Altaf et al. 2022b). However, the mechanisms by which melatonin interacts with other hormones in plants, particularly phytohormones, are not yet fully understood. Phytohormonal cross-talk with melatonin has emerged as an exciting area of research in plant biology. This chapter will provide an overview of the current state of research on phytohormonal cross-talk with melatonin in plants.

6.2 Biosynthesis and Metabolism of Melatonin

Melatonin is a small molecule that was first identified in animals as a sleep-inducing hormone. It is synthesized from tryptophan and is involved in the regulation of circadian rhythms in animals. However, it has since been discovered that plants also produce melatonin, and that it plays a role in various aspects of plant physiology (Tiwari et al. 2022a, b). Melatonin is involved in regulating plant growth and development, including seed germination, root growth, and flowering. It has also been implicated in responses to abiotic stresses such as drought, salt, and cold, as well as biotic stresses such as pathogen attack (Shi et al. 2016). The biosynthesis of melatonin in plants is similar to that in animals. It is synthesized from tryptophan via a series of enzymatic reactions, including decarboxylation, hydroxylation, and acetylation. Melatonin synthesis in plants is regulated by various environmental factors, including light, temperature, and stress. Two major pathways have been proposed based on the enzyme kinetics: One is the tryptophan/tryptamine/serotonin/N-acetylserotonin/melatonin pathway, which may occur under normal growth conditions; the other is the tryptophan/tryptamine/serotonin/5-methoxytryptamine/melatonin pathway, which may occur when plants produce large amounts of serotonin, for example, upon senescence.

6.2.1 Enzymatic Pathways for Melatonin Biosynthesis

Melatonin is a tryptophan-derived natural substance that is synthesized in practically all living species, including animals and plants (Reiter et al. 2013; Hardeland 2016). Melatonin functions as a signaling molecule to mediate the plant defense response against pathogen attack via the mitogen-activated protein kinase (MAPK) pathway (Arnao and Hernández-Ruiz 2014), in addition to its function as a biostimulator for plant growth and development (Lee et al. 2014; Lee and Back 2016). Furthermore, it is now well established that melatonin plays a role in mitigating many forms of abiotic stress, such as cold, dryness, heavy metals, and salt, all of which are common during plant growth in the field.

Melatonin biosynthesis from tryptophan requires four-step reactions. A total of six enzymes, that is, tryptophan decarboxylase (TDC), TPH, tryptamine 5-hydroxylase (T5H), serotonin N-acetyltransferase (SNAT), N-acetylserotonin methyltransferase (ASMT), and caffeic acid O-methyltransferase (COMT), are related to melatonin synthesis in plants (Fitzpatrick 1999).

Tryptophan, an amino acid, is converted into serotonin through the action of the enzyme tryptophan decarboxylase (TDC). Serotonin is then converted into N-acetylserotonin (NAS) by the action of serotonin N-acetyltransferase (SNAT). Finally, NAS is converted into melatonin by the action of N-acetylserotonin O-methyltransferase (ASMT). Melatonin metabolism in plants involves the action of several enzymes. One of these enzymes is melatonin 2-hydroxylase (M2H), which converts melatonin into 2-hydroxymelatonin. Another enzyme, melatonin 3-hydroxylase (M3H), converts melatonin into 3-hydroxymelatonin. Both of these metabolites have been detected in plant tissues.

The enzyme involved in the first step of melatonin synthesis is believed to be TDC, followed by T5H, because the decarboxylation step occurs in preference to the hydroxylation step in plants (pathway I). However, the inverse step, in which hydroxylation occurs first, is also present, although the corresponding TPH enzyme has yet to be identified (pathway III). Thus, the combination of three enzymes, TDC, T5H, and TPH, leads to the synthesis of serotonin, the key intermediate in melatonin synthesis. The synthesis of serotonin from tryptophan is highly active, which means greater metabolic flow for serotonin synthesis than for subsequent melatonin production from serotonin which also requires two enzymatic reactions. Due to the marked contrast in metabolic capacity, serotonin synthesis is massively induced up to 565 μg/g fresh weight (fw), whereas melatonin is induced to only 262 ng/g fw in detached rice leaves upon senescence (Byeon et al. 2012) this indicates a difference of more than three orders of magnitude in metabolic capacity between serotonin and melatonin synthesis at least in plants. These data clearly suggest that downstream melatonin synthesis from serotonin has extremely low metabolic capacity compared to upstream serotonin synthesis. Melatonin synthesis from serotonin is a two-step reaction, but involves three distinct enzymes, that is, SNAT, ASMT, and COMT. SNAT catalyzes serotonin into N-acetylserotonin, which is then converted into melatonin by either ASMT or COMT. As SNAT exhibits substrate affinity toward serotonin and 5-methoxytryptamine, SNAT reaction occurs first to produce N-acetylserotonin, which is then O-methylated to melatonin by ASMT/COMT. Similarly, ASMT and COMT also have substrate affinity toward serotonin and N-acetylserotonin, in which ASMT and COMT first methylate serotonin to 5-methoxytryptamine, followed by SNAT reaction to melatonin. In summary, serotonin can be catalyzed to N-acetylserotonin and 5-methoxytryptamine by SNAT and ASMT/COMT, followed by production of melatonin by ASMT/COMT and SNAT, respectively.

The order of enzyme reactions in the melatonin biosynthetic pathway changes the subcellular sites of intermediates and melatonin formation. For example, pathways I and II result in serotonin synthesis in the endoplasmic reticulum (ER), whereas pathways III and IV result in cytoplasmic production of serotonin. Melatonin synthesis occurs at chloroplasts when the final-step enzyme is SNAT, while ASMT/COMT is involved in the terminal reaction in the cytoplasm. Depending on the biosynthesis sites, the levels of serotonin and melatonin would be markedly influenced by the capacity of either anabolic flow or catabolic flow. Tryptophan and serotonin accumulate in high levels in the senesced leaves of rice, whereas tryptamine and *N*-acetylserotonin do not increase substantially. These events can be explained simply by the rapid conversion of tryptamine to serotonin by T5H, as well as a slow conversion of serotonin to *N*-acetylserotonin by SNAT (Kang et al. 2009a, 2010). On the other hand, marked accumulation of serotonin will not be achieved when enzyme(s) competing for serotonin as a substrate are present together at the same subcellular site. For example, serotonin is rapidly metabolized into phenylpropanoid amides, such as feruloylserotonin, by serotonin *N*-hydroxycinnamoyl transferase, which is expressed in the cytoplasm (Kang et al. 2009b). Melatonin can be rapidly metabolized into 2-hydroxymelatonin (2-OHMel) and cyclic 3-hydroxymelatonin (3-OHMel) by melatonin 2-hydroxylase (M2H) and melatonin 3-hydroxylase (M3H), respectively, when melatonin is present in the chloroplasts and cytoplasm, respectively (Byeon and Back 2015; Lee et al. 2016). The multiple pathways with different subcellular sites for melatonin production are thought to play important roles in maintaining steady-state levels of melatonin, as well as in the induction of melatonin synthesis in response to various stressors which allow plants to cope with adverse effects. This review will describe the enzymatic features of melatonin biosynthetic enzymes, their transcript levels, and possible metabolic engineering of the pathways in plants.

6.2.2 Regulation of Melatonin Metabolism

Melatonin metabolism is regulated by several factors, including environmental stimuli, light/dark cycles, and developmental stages. Enzymes involved in melatonin degradation, such as caffeic acid O-methyltransferase (COMT), play a crucial role in maintaining melatonin homeostasis.

6.3 Interactions Between Melatonin and Auxin

One of the best-studied examples of phytohormonal cross-talk with melatonin is the interaction between melatonin and auxin. Several studies have shown that melatonin can enhance auxin signaling and promote auxin-mediated processes such as cell elongation and lateral root formation. Melatonin has also been reported to regulate the expression of genes involved in auxin biosynthesis and transport.

6.3.1 Melatonin Modulates Auxin Biosynthesis and Transport

Auxin is primarily synthesized in the meristematic regions of plants, such as the shoot and root apices, and is subsequently transported to different parts of the plant through polar auxin transport (PAT). PAT involves the coordinated action of auxin efflux carriers (PIN proteins) and influx carriers (AUX/LAX proteins). PIN proteins are responsible for the directional efflux of auxin from cells, while AUX/LAX proteins facilitate auxin influx into cells. The balance between auxin efflux and influx is critical for proper auxin distribution and signaling in plants.

Melatonin has been shown to influence auxin biosynthesis by regulating the expression of genes involved in auxin synthesis (Arnao and Hernández-Ruiz 2016). For example, in Arabidopsis, melatonin treatment has been found to upregulate the expression of YUCCA (YUC) genes, which encode enzymes involved in the conversion of indole-3-pyruvic acid (IPyA) to indole-3-acetic acid (IAA), the primary active form of auxin. This upregulation of YUC gene expression leads to increased auxin biosynthesis, ultimately affecting plant growth and development. In addition to its effects on auxin biosynthesis, melatonin also modulates auxin transport (Altaf et al. 2021). Studies have demonstrated that melatonin treatment affects the expression and subcellular localization of PIN proteins, thereby influencing auxin efflux. For instance, melatonin treatment in Arabidopsis has been shown to enhance the expression and membrane localization of PIN1 and PIN2 proteins, resulting in increased auxin efflux from cells. These changes in PIN protein expression and localization are thought to be mediated by melatonin-induced calcium signaling.

Furthermore, melatonin has been shown to affect auxin influx by regulating the expression of AUX/LAX genes. In Arabidopsis, melatonin treatment has been found to upregulate the expression of AUX1 and LAX3 genes, leading to increased auxin influx into cells. This enhanced auxin influx can influence various developmental processes, such as root growth and tropic responses (Tan et al. 2020). Melatonin influences auxin biosynthesis and transport processes. It can regulate the expression of auxin biosynthetic genes and affect the activity of auxin efflux carriers, thereby modulating auxin distribution in plants.

6.3.2 Cross-Talk Between Melatonin and Auxin Signaling Pathways

The interaction between melatonin and auxin signaling pathways involves a complex network of molecular events that modulate plant growth and development (Lal et al. 2022). Several studies have elucidated the cross-talk between these two hormone systems at the molecular level.

One of the key mechanisms underlying the cross-talk between melatonin and auxin signaling pathways is through the regulation of gene expression. Melatonin has been shown to modulate the expression of genes involved in auxin biosynthesis, transport, and signaling. For example, melatonin treatment has been found to upregulate the expression of auxin biosynthesis-related genes, such as YUC and TAA1, in Arabidopsis. This upregulation of gene expression leads to increased auxin levels and affects auxin-mediated processes.

Melatonin also influences auxin signaling by interacting with components of the auxin signaling pathway (Tiwari et al. 2021b). Studies have demonstrated that melatonin treatment can affect the stability and activity of key transcription factors involved in auxin signaling, such as AUXIN RESPONSE FACTORs (ARFs) and AUXIN/INDOLE-3-ACETIC ACID (AUX/IAA) proteins. Melatonin has been shown to promote the degradation of AUX/IAA proteins, which allows ARFs to activate the expression of downstream auxin-responsive genes (Liang et al. 2021). This interaction between melatonin and auxin signaling components provides a mechanism for the regulation of auxin-responsive gene expression and subsequent physiological responses.

6.3.3 Roles of Melatonin and Auxin in Plant Growth and Development

Both melatonin and auxin play essential roles in the regulation of plant growth and development. Melatonin influences various aspects of plant growth, including seed germination, root and shoot growth, flowering, and fruit ripening. It has been shown to promote seed germination under adverse conditions, such as salinity and drought stress. Melatonin also enhances root growth and lateral root formation, which are crucial for nutrient acquisition and water uptake.

Auxin, on the other hand, regulates diverse developmental processes, such as embryogenesis, organogenesis, tropic responses, and senescence. It promotes cell elongation and division, which are essential for organ growth (Chourasia et al. 2021). Auxin gradients control tropic responses, such as phototropism and gravitropism, allowing plants to adapt to their environment. Moreover, auxin is involved in leaf senescence, regulating the timing of leaf aging and nutrient remobilization.

The cross-talk between melatonin and auxin signaling pathways contributes to the coordination of these hormone systems in plant growth and development (Zhao and Christensen 2021). For instance, melatonin-induced changes in auxin biosynthesis and transport can influence root architecture and lateral root development. Melatonin has been shown to increase primary root length and enhance lateral root formation by modulating auxin levels and distribution.

Additionally, the interaction between melatonin and auxin signaling pathways can affect flowering time and floral organ development. Studies have revealed that melatonin treatment delays flowering time and alters floral organ morphology in Arabidopsis (Zhang et al. 2014). These effects are associated with changes in auxin signaling and the expression of floral regulatory genes.

In conclusion, melatonin and auxin have emerged as important regulators of plant growth and development. The cross-talk between these hormone systems influences auxin biosynthesis, transport, and signaling, ultimately affecting various aspects of plant physiology. Understanding the intricate relationship between melatonin and auxin signaling pathways will contribute to the development of novel strategies for enhancing crop productivity and improving plant stress tolerance.

6.4 Melatonin and Gibberellins

Gibberellins (GAs) are essential regulators of plant growth and development. They control processes such as seed germination, stem elongation, leaf expansion, and flower development. Melatonin can modulate GA biosynthesis and signaling pathways (Yamaguchi 2008). It affects the expression of GA biosynthetic and catabolic genes, as well as the activity of GA receptors and transcription factors involved in GA-responsive gene expression. The interplay between melatonin and GAs influences various growth and developmental processes, including seed germination, stem elongation, flowering time, and fruit development. The biosynthesis and metabolism of GAs are complex processes that regulate various aspects of plant growth and development. Melatonin influences GA signaling by modulating GA biosynthesis and the activity of GA-responsive genes.

6.4.1 Gibberellin Biosynthesis and Metabolism

Gibberellins are a class of plant hormones that play a crucial role in various aspects of plant growth and development, including seed germination, stem elongation, flowering, and fruit development. The biosynthesis and metabolism of GAs are complex processes involving multiple enzymes and regulatory steps.

The biosynthesis of GAs begins with the conversion of geranylgeranyl diphosphate (GGDP) into ent-kaurene, which is catalyzed by the enzyme ent-copalyl diphosphate synthase (CPS). This step is considered the first committed step in the

GA biosynthetic pathway (Sakamoto and Yokota 2004). The ent-kaurene is then converted into GA12-aldehyde by a series of enzymatic reactions, including ent-kaurene oxidase (KO) and ent-kaurenoic acid oxidase (KAO). GA12-aldehyde is further converted into bioactive GAs, such as GA1 and GA4, through several steps, including 3β-hydroxylation, 13-hydroxylation, and 20-oxidation.

The metabolism of GAs involves both inactivation and deactivation processes. One of the major inactivation pathways is the conversion of active GAs into inactive forms, such as GA8 and GA34, through the action of GA 2-oxidases (GA2ox). These enzymes catalyze the removal of the C-2 and C-3 hydroxyl groups from the GA molecule. Additionally, GA20-oxidases (GA20ox) are responsible for the deactivation of GAs by converting them into inactive forms, such as GA29 and GA29-diol.

The regulation of GA biosynthesis and metabolism is tightly controlled at multiple levels. The expression of genes encoding enzymes involved in GA biosynthesis and metabolism is regulated by various factors, including light, temperature, hormones, and developmental cues. Transcription factors, such as DELLA proteins, play a crucial role in the regulation of GA biosynthesis and signaling by binding to and inhibiting the activity of key regulators of GA biosynthesis, such as GA3ox and GA20ox.

6.4.2 Influence of Melatonin on Gibberellin Signaling

Melatonin is a multifunctional molecule found in plants and animals, including humans (Kumar et al. 2022). It has been extensively studied for its role in regulating various physiological processes, including circadian rhythms, stress responses, and immune functions. Emerging evidence suggests that melatonin also influences GA signaling, thereby affecting plant growth and development (Tiwari et al. 2022a, b; Devi et al. 2022a, b).

Studies have shown that melatonin can modulate GA biosynthesis by regulating the expression of key genes involved in GA metabolism. For example, in rice (Oryza sativa), exogenous application of melatonin has been found to upregulate the expression of GA biosynthesis genes, such as CPS, KO, and GA3ox, leading to increased GA levels and enhanced plant growth (Li et al. 2015). Similarly, in Arabidopsis thaliana, melatonin treatment has been shown to upregulate the expression of GA biosynthesis genes, resulting in increased GA content and promotion of seed germination and seedling growth (Park et al. 2013a).

Melatonin also influences GA signaling by modulating the activity of GA-responsive genes. In rice, melatonin treatment has been found to enhance the expression of GA-responsive genes, such as GA-induced protein (GIP1) and GA receptor (GID1), which are involved in GA signaling pathways. This suggests that melatonin can enhance GA responsiveness and promote GA-mediated physiological responses.

6.4.3 Effects of Melatonin–Gibberellin Interactions on Plant Growth and Development

The interactions between melatonin and GAs have significant effects on plant growth and development. Studies have demonstrated that the combined application of melatonin and GAs can have synergistic effects on various aspects of plant growth.

One of the main effects of melatonin–GA interactions is the promotion of seed germination and seedling growth (Tiwari et al. 2021a). Exogenous application of melatonin and GAs has been shown to enhance seed germination rates and promote early seedling growth in various plant species. The synergistic effect of melatonin and GAs on seed germination is believed to be due to the increased expression of GA biosynthesis genes and enhanced GA signaling, resulting in improved embryo growth and mobilization of seed reserves.

Melatonin–GA interactions also influence stem elongation and plant height. In some plant species, melatonin treatment has been found to promote stem elongation and increase plant height by enhancing GA biosynthesis and signaling (Zhang et al. 2014). This effect is particularly evident in elongating internodes and can contribute to improved crop productivity and biomass accumulation.

Furthermore, the combined application of melatonin and GAs can enhance flowering and fruit development. In several plant species, melatonin treatment has been shown to promote flowering and increase the number of flowers and fruits. This effect is mediated through the regulation of GA biosynthesis and signaling, which influences the expression of genes involved in floral induction and development.

6.5 Cross-Talk Between Melatonin and Abscisic Acid

Melatonin is a hormone primarily known for its role in regulating sleep and circadian rhythms. However, emerging research suggests that melatonin also plays a crucial role in plant physiology, including the regulation of abscisic acid (ABA) biosynthesis and signaling. ABA is a key phytohormone involved in various physiological processes, particularly in plant responses to stress (Lal et al. 2021; Kumar et al. 2021a, b). This article explores the intricate relationship between melatonin and ABA and their impact on plant stress responses. Melatonin can regulate ABA biosynthesis by modulating the expression of ABA biosynthetic genes. It also interacts with ABA signaling components, such as ABA receptors and transcription factors, influencing ABA-responsive gene expression.

Melatonin enhances plant tolerance to abiotic stress by interacting with ABA signaling pathways. It regulates stomatal closure, ROS scavenging, and the expression of stress-responsive genes, thereby promoting stress adaptation.

Melatonin and ABA are two important phytohormones that play crucial roles in plant physiology, particularly in stress responses. Melatonin positively regulates ABA biosynthesis and signaling, leading to increased ABA levels in plants (Arnao and Hernández-Ruiz 2019). The synergistic actions of melatonin and ABA enhance plant stress tolerance by activating stress-responsive genes, modulating ABA signaling, and maintaining redox homeostasis. Understanding the intricate relationship between melatonin and ABA provides valuable insights into plant stress responses and opens avenues for developing novel strategies to improve crop productivity under challenging environmental conditions (Naga et al. 2021a, b).

6.5.1 Melatonin Regulation of Abscisic Acid Biosynthesis and Signaling

Abscisic Acid Biosynthesis and Signaling ABA biosynthesis pathways vary among different plant species, but the core pathway involves the conversion of carotenoids to xanthoxin and subsequent steps (Kumar et al. 2021a, b). ABA biosynthesis is regulated by various environmental cues, including drought, high salinity, and low temperature (Wei et al. 2019). Once synthesized, ABA regulates gene expression by binding to specific receptors, leading to downstream signaling events. ABA signaling involves several components, such as protein phosphatases, kinases, and transcription factors, which collectively regulate ABA-responsive gene expression.

Melatonin Regulation of ABA Biosynthesis Studies have demonstrated that melatonin can regulate ABA biosynthesis at multiple levels. Melatonin treatment has been shown to enhance the expression of genes involved in ABA biosynthesis, such as 9-cis-epoxycarotenoid dioxygenase (NCED), which is a key enzyme in ABA synthesis. In addition, melatonin can also upregulate the expression of ABA receptor genes, thus influencing ABA signaling. These findings suggest that melatonin positively regulates ABA biosynthesis, leading to increased ABA levels in plants.

6.5.2 Melatonin-Mediated Abscisic Acid Responses During Stress

Melatonin and ABA act synergistically to enhance plant stress tolerance. Under stress conditions such as drought, salinity, and extreme temperatures, both melatonin and ABA levels increase in plants. Melatonin has been shown to promote ABA accumulation in response to stress by upregulating ABA biosynthesis genes. Increased ABA levels, in turn, activate stress-responsive genes and induce adaptive responses to mitigate the detrimental effects of stress (Park et al. 2013b).

Melatonin also influences ABA signaling by modulating the expression of ABA receptor genes and downstream components of the ABA signaling pathway. It has been demonstrated that melatonin can enhance the sensitivity of ABA receptors, thereby amplifying ABA signaling. This interaction between melatonin and ABA signaling pathways helps plants to better cope with stress conditions.

Furthermore, melatonin's antioxidant properties play a crucial role in plant stress responses. Stressful conditions often lead to the generation of reactive oxygen species (ROS) in plants, causing oxidative damage. Melatonin acts as a potent scavenger of ROS and helps maintain redox homeostasis. It also enhances the activities of antioxidant enzymes, such as superoxide dismutase and catalase, further enhancing the plant's antioxidant defense system.

6.6 Melatonin and Ethylene

Ethylene is a key plant hormone involved in various physiological processes, including growth, development, and stress responses. Its biosynthesis and signaling pathways have been extensively studied. In recent years, the role of melatonin, a multifunctional molecule, has gained attention in modulating ethylene pathways and influencing plant defense and senescence processes (Alexander and Grierson 2002). Additionally, the role of melatonin–ethylene interactions in plant defense and senescence is discussed, highlighting the potential mechanisms underlying these interactions. Ethylene is a crucial plant hormone involved in various processes, including fruit ripening, senescence, and response to biotic and abiotic stresses (Chang and Stadler 2001). Melatonin can regulate ethylene biosynthesis and signaling by modulating the expression of ethylene biosynthetic genes, ethylene receptors, and downstream transcription factors. The cross-talk between melatonin and ethylene influences plant defense responses against pathogens, as well as leaf and flower senescence.

6.6.1 Ethylene Biosynthesis and Signaling

Ethylene is a gaseous plant hormone that plays a crucial role in various developmental and physiological processes. It regulates growth, senescence, fruit ripening, and responses to biotic and abiotic stresses. The biosynthesis and signaling pathways of ethylene are highly complex and tightly regulated. In this article, we will explore the mechanisms of ethylene biosynthesis and signaling, highlighting the key enzymes and regulators involved.

Ethylene is derived from the amino acid methionine, which is converted to S-adenosylmethionine (SAM) by the enzyme SAM synthetase. SAM is then converted to 1-aminocyclopropane-1-carboxylic acid (ACC) by the enzyme ACC synthase (ACS) (Ma et al. 2013). ACS is the rate-limiting enzyme in ethylene biosynthesis and is tightly regulated at the transcriptional and post-translational levels.

Once ACC is formed, it is further converted to ethylene by the enzyme ACC oxidase (ACO). ACO is also regulated transcriptionally and post-translationally (Van de Poel and Van Der Straeten 2014). The conversion of ACC to ethylene involves the production of an intermediate, cyanide, which is detoxified by the enzyme β-cyanoalanine synthase (CAS). This detoxification step prevents the accumulation of toxic levels of cyanide in plant tissues.

Ethylene signaling is mediated by a family of receptors known as ethylene receptors. In Arabidopsis thaliana, a model plant species, there are five ethylene receptors: ETR1, ERS1, ETR2, ERS2, and EIN4. These receptors are localized to the endoplasmic reticulum and function as negative regulators of ethylene responses. In the absence of ethylene, the receptors are active and inhibit the downstream signaling pathway.

When ethylene binds to the receptors, it triggers a series of events that lead to the inactivation of the receptors and the activation of the downstream signaling pathway. The receptors interact with the Raf-like kinase CTR1, which phosphorylates and inactivates a downstream protein called EIN2. Inactivation of EIN2 leads to the stabilization and nuclear translocation of a transcription factor called EIN3/EIL1. EIN3/EIL1 regulates the expression of a wide array of ethylene-responsive genes, including those involved in fruit ripening, senescence, and defense responses. EIN3/EIL1 interacts with other transcription factors and co-regulators to modulate gene expression in response to ethylene. The downstream targets of EIN3/EIL1 include ethylene response factors (ERFs), which are a large family of transcription factors that directly regulate ethylene-responsive genes.

In addition to its role in development and senescence, ethylene is also involved in plant defense responses. It can induce the production of defense-related metabolites, such as phytoalexins and pathogenesis-related (PR) proteins, to protect plants against pathogens. Ethylene also regulates the expression of genes involved in the production of reactive oxygen species (ROS), which are important signaling molecules in plant defense. Overall, ethylene biosynthesis and signaling pathways are tightly regulated to ensure precise control over plant growth, development, and responses to environmental cues. Understanding the mechanisms underlying ethylene biosynthesis and signaling is of great importance for the improvement of crop productivity, disease resistance, and post-harvest quality.

6.6.2 Melatonin-Induced Modulation of Ethylene Pathways

Melatonin, a hormone originally identified in animals, has been found to be present in plants as well. It plays a vital role in plant growth, development, and responses to environmental stresses. In recent years, research has revealed the involvement of melatonin in the modulation of ethylene pathways. This article explores the effects of melatonin on ethylene biosynthesis, signaling, and their interactions.

Ethylene biosynthesis is regulated by various factors, including the rate-limiting enzyme ACC synthase (ACS). Several studies have shown that melatonin can modulate the expression and activity of ACS. For instance, in tomato (Solanum lycopersicum), exogenous melatonin treatment significantly increased ACS activity, leading to enhanced ethylene production and accelerated fruit ripening. Similar findings have been reported in other plant species, such as apple (Malus domestica) and cucumber (Cucumis sativus) (Wei et al. 2018).

Melatonin also influences ethylene signaling pathways. It has been observed that melatonin treatment can upregulate the expression of ethylene receptors, such as ETR1 and ERS1, thereby enhancing ethylene perception and downstream signaling. Moreover, melatonin can activate downstream transcription factors, such as EIN3/

EIL1, which regulate the expression of ethylene-responsive genes. These findings suggest that melatonin promotes ethylene signaling and amplifies the ethylene response in plants.

Furthermore, melatonin can interact with other components of the ethylene pathway to modulate their activities. One such interaction involves the modulation of enzyme activities involved in ethylene metabolism. Studies have shown that melatonin treatment can inhibit the activity of ACC oxidase (ACO), the enzyme responsible for the conversion of ACC to ethylene. This leads to reduced ethylene production and delayed fruit ripening in various plant species.

Additionally, melatonin has been found to affect the expression of genes encoding ethylene biosynthesis and signaling enzymes. For example, melatonin treatment can upregulate the expression of ACS genes and downregulate the expression of ACO genes (Zander et al. 2010). These changes in gene expression contribute to the overall modulation of ethylene pathways by melatonin.

The modulation of ethylene pathways by melatonin has important implications in plant physiology and stress responses. For instance, melatonin-induced delay in fruit ripening can prolong the shelf life of harvested fruits and reduce post-harvest losses. Melatonin-mediated enhancement of ethylene signaling can also promote plant defense responses against pathogens, as ethylene plays a crucial role in plant immunity.

In conclusion, melatonin has emerged as a key regulator of ethylene pathways in plants. It affects ethylene biosynthesis, signaling, and their interactions, thereby modulating various aspects of plant growth, development, and stress responses. Further research is needed to elucidate the precise mechanisms underlying melatonin–ethylene interactions and their significance in plant biology.

6.6.3 Role of Melatonin–Ethylene Interactions in Plant Defense and Senescence

The interactions between melatonin and ethylene play a crucial role in plant defense responses and senescence processes. Melatonin, a hormone present in both animals and plants, and ethylene, a gaseous hormone in plants, regulate various physiological and molecular processes (Arnao and Hernández-Ruiz 2018). In this article, we explore the role of melatonin–ethylene interactions in plant defense and senescence, shedding light on their molecular mechanisms and implications.

Plant defense responses are crucial for protecting plants against various biotic stresses, including pathogen attack and herbivory. Both melatonin and ethylene are involved in the regulation of defense responses. Studies have shown that melatonin treatment can induce the expression of genes involved in defense pathways, such as those encoding pathogenesis-related (PR) proteins and defense-related enzymes. Melatonin can also enhance the production of reactive oxygen species (ROS), which play a crucial role in plant defense (Chen et al. 2019).

Ethylene, on the other hand, is a well-known regulator of defense responses. It induces the expression of defense-related genes, such as those encoding PR proteins, and activates various defense mechanisms, including the production of antimicrobial compounds. Ethylene also regulates the hypersensitive response (HR), a form of programmed cell death that restricts pathogen spread.

The interaction between melatonin and ethylene in defense responses has been observed in several studies. Melatonin treatment has been shown to enhance the expression of ethylene biosynthesis and signaling genes, leading to increased ethylene production and amplified defense responses (Liu et al. 2021). Furthermore, melatonin can modulate the activity of enzymes involved in ethylene metabolism, such as ACC oxidase (ACO), resulting in the regulation of ethylene levels.

In addition to defense responses, melatonin–ethylene interactions also play a role in plant senescence. Senescence is a highly regulated process that involves the programmed degradation of cellular components and the recycling of nutrients. Ethylene is a key regulator of senescence, promoting leaf yellowing, chlorophyll degradation, and the breakdown of macromolecules.

Melatonin has been found to modulate ethylene-mediated senescence processes. It can delay leaf senescence and maintain chlorophyll content in various plant species. Melatonin treatment has also been shown to downregulate the expression of senescence-related genes, including those encoding senescence-associated proteins and proteases involved in protein degradation during senescence. The molecular mechanisms underlying melatonin–ethylene interactions in defense and senescence are complex and not fully understood. It is likely that melatonin acts upstream or downstream of ethylene signaling components to modulate their activities. Further research is needed to unravel the precise mechanisms and signaling pathways involved in these interactions.

Understanding the role of melatonin–ethylene interactions in plant defense and senescence has significant implications for agriculture and crop improvement. Manipulating these interactions may lead to the development of strategies to enhance plant resistance to pathogens and delay senescence, thus improving crop yield and post-harvest quality.

6.7 Melatonin and Brassinosteroids

Brassinosteroids (BRs) are important regulators of plant growth and development. They control processes such as cell elongation, vascular development, and stress responses.

Brassinosteroids, a class of plant hormones, play crucial roles in regulating various physiological and developmental processes. The biosynthesis of BRs involves multiple enzymatic reactions, including the conversion of campesterol to the active BR molecule, castasterone. Once synthesized, BRs transmit signals through a receptor-mediated pathway, leading to diverse downstream responses.

Melatonin can interfere with BR biosynthesis, affecting the expression of BR biosynthetic genes and the activity of BR signaling components, including receptors and transcription factors. The combined actions of melatonin and BRs influence various aspects of plant growth, including stem elongation, root development, and stress tolerance.

However, recent research has shed light on the interaction between melatonin, a multifunctional molecule, and BR signaling. Melatonin has been found to interfere with BR pathways at multiple levels, influencing BR biosynthesis, signaling, and downstream gene expression. The intricate cross-talk between melatonin and BRs has significant implications for plant growth, stress tolerance, and adaptive responses. BR biosynthesis involves several enzymatic reactions, starting from the conversion of campesterol to the intermediate molecule, teasterone. Subsequent hydroxylation, oxidation, and reduction reactions yield the bioactive BR molecule, castasterone. Key enzymes involved in these processes include CYP90D1, CYP90B1, DET2, and ROT3. BR biosynthesis is tightly regulated by multiple factors, such as light, temperature, hormone interactions, and genetic factors. For instance, light signals can regulate the expression of BR biosynthetic genes, thereby modulating BR levels in response to environmental cues.

6.7.1 Melatonin Interference with Brassinosteroid Pathways

Melatonin Biosynthesis Melatonin biosynthesis in plants involves multiple enzymatic steps, including the conversion of tryptophan to serotonin, followed by its conversion to N-acetylserotonin and subsequent conversion to melatonin. Key enzymes involved in melatonin biosynthesis include serotonin N-acetyltransferase (SNAT) and N-acetylserotonin methyltransferase (ASMT).

Interference with BR Biosynthesis Melatonin has been shown to inhibit the expression and activity of key enzymes involved in BR biosynthesis, such as CYP90B1 and CYP90D1. This interference leads to a reduction in BR levels, subsequently influencing plant growth and development.

Combined Effects of Melatonin and Brassinosteroids on Plant Growth and Stress Tolerance Studies have reported that exogenous application of melatonin and BRs individually promotes plant growth. However, their combined application has demonstrated synergistic effects, leading to enhanced growth parameters such as plant height, leaf area, and biomass accumulation. Both melatonin and BRs play crucial roles in plant stress responses. The combined application of melatonin and BRs has shown significant improvements in stress tolerance, including enhanced antioxidant capacity, reduced oxidative damage, improved photosynthesis, and increased drought and salt tolerance.

6.8 Interplay Between Melatonin and Jasmonates

Jasmonates (JAs) are crucial phytohormones involved in plant defense against biotic stresses, as well as regulating processes such as growth and development. Melatonin can modulate JA biosynthesis and signaling by regulating the expression of JA biosynthetic genes, JA receptors, and transcription factors involved in JA-responsive gene expression. The interplay between melatonin and JAs influences plant defense responses against pathogens and herbivores. Melatonin enhances JA-mediated defense gene expression, production of defense metabolites, and systemic acquired resistance.

6.9 Cross-Talk Between Melatonin and Cytokinin

Cytokinins, a class of plant hormones, play pivotal roles in various physiological processes, including cell division, growth, and development. Over the years, research has highlighted the intricate cross-talk between melatonin and cytokinins, indicating their intertwined roles in regulating plant growth, stress responses, and circadian rhythms (Kurepin et al. 2020). This chapter provides an overview of the current understanding of the cross-talk between melatonin and cytokinins in plants, discussing their mutual regulation and implications in plant physiology. Both melatonin and cytokinins play critical roles in plant physiology, and recent research suggests an intricate interplay between these two signaling molecules.

6.9.1 Cytokinin Biosynthesis

Cytokinins are synthesized through two primary pathways: the isoprenoid and the adenylate pathways. The isoprenoid pathway involves the conversion of isopentenyl diphosphate (IPP) into isopentenyladenosine 5′-monophosphate (iPMP), while the adenylate pathway synthesizes cytokinins from ATP. Key enzymes in cytokinin biosynthesis include isopentenyltransferases (IPTs) and adenylate isopentenyltransferases (AIs).

6.9.2 Melatonin and Cytokinin Signaling Pathways

Melatonin signaling in plants involves receptors, such as calmodulin-like proteins and G-protein-coupled receptors, which trigger downstream events, including the modulation of gene expression and activation of antioxidant defense pathways. On the other hand, cytokinin signaling primarily occurs through a two-component system involving histidine kinases, histidine phosphotransfer proteins, and response regulators. Studies have revealed that melatonin positively influences cytokinin biosynthesis, leading to increased cytokinin levels in various plant tissues (Werner et al. 2003). Melatonin application has been shown to enhance cytokinin biosynthesis-related gene expression, resulting in improved plant growth, stress tolerance, and delayed senescence.

The interplay between melatonin and cytokinins significantly impacts plant growth and development. The mutual regulation between these signaling molecules influences processes such as cell division, shoot formation, root development, and flowering. Studies have shown that the exogenous application of melatonin and cytokinins promotes plant growth, increases leaf area, and enhances shoot and root biomass.

6.9.3 Stress Responses

Both melatonin and cytokinins play crucial roles in plant stress responses. Melatonin acts as a potent antioxidant and free radical scavenger, protecting plants against oxidative stress induced by various environmental factors. Cytokinins, on the other hand, regulate stress-responsive genes and modulate the expression of stress-related proteins. The cross-talk between melatonin and cytokinins contributes to enhanced stress tolerance, promoting plant survival under adverse conditions.

6.10 Conclusion and Future Perspectives

In recent years, the investigation of the intricate communication between different signaling molecules has gained significant attention in various biological systems. In conclusion, the cross-talk between melatonin and phytohormones in plants represents a fascinating area of research. The interaction between melatonin and auxins, cytokinins, gibberellins, abscisic acid, and ethylene plays a crucial role in regulating various physiological processes in plants, including growth and development, stress responses, and the circadian rhythm. However, many questions regarding the mechanisms and biological functions of this cross-talk remain unanswered. Further research is needed to elucidate the precise molecular mechanisms by which melatonin interacts with phytohormones and to uncover additional phytohormones that may interact with melatonin. Additionally, more studies are needed to explore the potential applications of melatonin and phytohormonal cross-talk in agriculture, such as crop improvement and stress tolerance.

6.10.1 Integration of Melatonin into the Phytohormonal Network

The cross-talk between melatonin and other phytohormones reveals the integration of melatonin into the complex hormonal network that regulates plant growth, development, and stress responses. The intricate interplay between brassinosteroid biosynthesis and signaling, and melatonin interference in BR pathways, highlights the complexity of plant hormone regulation.

6.10.2 Harnessing Melatonin–Phytohormone Interactions for Crop Improvement

Understanding the interactions between melatonin and phytohormones provides opportunities for harnessing these interactions to enhance plant productivity, stress tolerance, and crop improvement strategies.

6.10.3 Future Directions in Research on Phytohormonal Cross-Talk with Melatonin

Further research is needed to unravel the precise mechanisms underlying the cross-talk between melatonin and other phytohormones. Investigations into the effects of melatonin–phytohormone interactions under various environmental conditions and the identification of specific signaling components involved will contribute to a comprehensive understanding of melatonin's role in plant physiology. Understanding the interplay between melatonin and Hormones will provide valuable insights into plant adaptation strategies and may pave the way for the development of innovative approaches to improve crop productivity, stress tolerance as well as in field of medicine and chronobiology, paving the way for potential therapeutic applications and improved crop production in the future.

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Interaction of Melatonin with Reactive Oxygen Species in Plants

7

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Abstract

Climate change has resulted in a steady and irreversible shift in the global climate, and occurrences like salinity, drought, temperature rises, high luminous intensity, and ultraviolet radiations are getting more intense and extended over time. The aforementioned spells have subjected agricultural crops to perpetual and unprecedented stress, as evidenced by an increase in the generation of deadly reactive species, including reactive oxygen species (ROS) in plant tissues. The latter are routinely synthesized as products of various aerobic redox reactions and serve as plant's secondary messengers in response to environmental and biotic stressors. However, exceeding the cellular concentration threshold leads to irreversible damages to biomolecules, which eventually amalgamate to cell death. In its attempt maintain cellular redox homeostasis, plants have evolved sophisticated antioxidant machinery to fine-tune ROS production and degradation rates.

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Among antioxidant compounds; the *N*-acetyl-5-methoxytryptamine (Melatonin), a multi-purpose and widespread compound has recently drawn the attention of plant physiologists. Melatonin acts by quenching excess ROS generation in a direct manner, or indirectly as a signal molecule, by modulating the expression of critical plant stress-defense genes. Several studies have shown that *N*-acetyl-5-methoxytryptamine interacts with ROS, which are well-known signal molecules, to activate plants' physiological and biochemical responses to varied stressful circumstances via intricate signaling networks. In this chapter, we dealt with ROS formation and the damage they cause to biomolecules, ROS functions in calcium-dependent cell-to-cell signaling, and ROS-mediated cellular signaling via the mitogen-activated protein kinases (MAPKs) pathway. Furthermore, the ROS regulation of certain transcription factors, as well as the melatonin-mediated redox homeostasis via its antioxidant potential and role of the respiratory burst oxidase homologs (RBOHs) are examined. Drilling into this intricate interaction will help design long-lasting strategies to sustainably overcome the deadly effects of environmental stresses to agricultural plants.

Keywords

Oxidative stress · Second messengers · Reactive oxygen species · Melatonin · Interplay redox homeostasis

7.1 Introduction

Climate change is a worldwide and ongoing phenomenon that is altering the Earth's climate. The primary consequence of this phenomena is a rise in world temperature, which causes drought, salinity stress, chilly, and heat, as well as an upsurge of biotic stressors caused by organisms such as filamentous fungi, yeasts, bacteria, and viruses. One of the direct setbacks are dramatically shortened crop productivity, with darker figure to come (Martinez-Feria et al. 2018). To survive, plants have evolved complex regulatory networks comprising molecular and physiological restructuring across time (Zhang et al. 2022b). One of the earliest and fastest plant reactions to hostile conditions is the excessive production of reactive chemical substances such as ROS, H_2O_2 (hydrogen peroxide), ($O_2^{\bullet -}$) (superoxide anion), $^1O_2$ (singlet oxygen), and $^{\bullet}OH$ (hydroxyl radical) (Qi et al. 2018; Ma et al. 2020; Sachdev et al. 2021). Reactive oxygen species are double-edged swords, with functions dependent on their cellular concentration. Their synthesis is moderate under normal physiological circumstances and is mostly related to cell signaling mechanisms. nonetheless, under conditions of stress, they are massively produced and accumulated (Zhou et al. 2022). As a result, redox homeostasis is disrupted, causing harm to cellular constituents such as proteins, carbohydrates, nucleic acids, membranous structures, photosynthetic pigments, and hormones. This may lead to programmed cell death due to oxidative stress (Bose et al. 2014; Zhou et al. 2022). Plants have evolved complex antioxidant systems to manage ROS homeostasis in response to oxidative stress as a way for them to thrive (Foyer and Noctor 2005; Sachdev et al. 2021). To buffer this highly reactive species, plants synthesize and activate enzymatic (catalases, superoxide dismutases, ascorbate and glutathione peroxidases, peroxidases) and non-enzymatic (ascorbic acid, peroxy-redoxins, alkaloids, non-protein amino acids glutathione (GSH) and melatonin) antioxidants (Foyer and Noctor 2005; Matamoros and Becana 2021). Phytomelatonin or *N*-acetyl-5-methoxytryptamine commonly called melatonin (MEL) was discovered in plants for the first time in 1995 (Hattori et al. 1995; Dubbels et al. 1995). Since then, several research have been undertaken to investigate what it does in plants, confirming its protective capabilities as a pleiotropic signaling molecule. Also, MEL can stimulate seed germination, control plant growth and development, increase flowering, and postpone leaf senescence in harsh environmental circumstances, among other things. Melatonin operates as an indirect stress regulator by influencing gene expression through putative transcription factors (Arnao and Hernández-Ruiz 2020). Moreover, melatonin acts as a direct antioxidant in the management of ROS levels by modulating redox enzymes and metabolites (Lee and Back 2016b; Gu et al. 2017; Tousi et al. 2020). Exogenous melatonin application can improve plant tolerance to stress (for example, drought, salt, heat, cold, waterlogging, and heavy metal toxicity) by modulating the inherent MEL biosynthesis (Weeda et al. 2014; Zhang et al. 2015; Moustafa-Farag et al. 2020; Sun et al. 2021). Melatonin can also interact with plant hormones such jasmonic acid (JA), salicylic acid (SA), cytokinin (CK), indoleacetic acid (IAA), gibberellic acid (GA), ethylene (ET), abscisic acid (ABA), brassinosteroid (BR), etc. (Arnao and Hernández-Ruiz 2020). This compound has received increased scientific interest in recent years due to the rising detrimental impacts of climate change and pollution in agriculture, owing to its preventive abilities. Over the last decade, significant progress has been made in general understanding of the functions of melatonin in plants. Updated data highlighting the interplay between ROS and melatonin for the reestablishment of cellular redox homeostasis are highly advocated. In this chapter, we attempted to tackle what is currently known by gathering the abundant but very divergent knowledge generated in this scientific field over the last decades, with a special emphasis on possible signaling pathways linking melatonin and ROS in the prospect of mitigating the deleterious effects of multiple stresses in agricultural crops.

7.2 Reactive Species: Definition and Types

Reactive species (RS) are molecules that, due to their redox state, have a high ability to react with biological molecules. Among RS, reactive nitrogen species (RNS) and ROS are metabolically closed. RNS includes peroxynitrite (ONOO) and *S*-nitrosoglutathione (GSNO), both of which are derive from the nitric oxide ($NO^{\bullet}$) radical (Choudhury et al. 2017). Despite the fact that their biosynthesis occurs under normal physiological circumstances, these two chemical families are prone to uncontrolled overproduction under extreme circumstances, resulting in cellular nitro-oxidative damage that impairs cell functioning and finally leads to death (Brannan 2010). ROS, for instance, are intermediates with distinct redox state that originate from ambient oxygen (O_2). There are various types of ROS, each with a particular reactivity and oxidizing capacity (Choudhury et al. 2017; Huang et al. 2019). In plants, they are synthesized organelles via metabolic processes involving oxidase and peroxidase enzymes, in variable amounts depending on plant organ and developmental stage (Janků et al. 2019). Oxygen (O_2) is created during photosynthetic metabolism as a result of varying excitation states of chlorophylls and the activity of photosystem II reaction center (Roach and Krieger-Liszkay 2014; Janků et al. 2019). The most persistent ROS is hydrogen peroxide (H_2O_2), with a strong intracellular diffusibility (Kim et al. 2018; Arnao and Hernández-Ruiz 2019). It is generated by the activity of the superoxide dismutase (SOD) by the extinction of O_2 as a result of the cleavage of the double bond of H_2O_2 through the Fenton reaction (Arnao and Hernández-Ruiz 2019; Huang et al. 2019) .

7.2.1 Sub-cellular Compartmentalization of ROS Biosynthesis

Plant cells produce ROS via mitochondria, chloroplasts, plasma membranes, peroxisomes, and the cell wall. ROS has been shown to be produced under both normal and stressful environments (Corpas et al. 2015). In the presence of light, ROS are preferentially synthesized by peroxisomes and chloroplasts, but in the absence of light, mitochondria are the sole organelle responsible for generating ROS.

7.2.1.1 Chloroplastic ROS Production

Chloroplasts are the most common plant organelles bearing all of the biochemical machinery required to convert light energy into chemical energy via photosynthesis. The chloroplast is the primary location of cellular ROS production. The two primary processes involved in ROS formation during photosynthesis are the direct photoreduction of O_2 to the superoxide radical by auto-oxidation of reduced ferredoxin at photosystem I (PSI) and plastoquinone (PQ) level in photosystem PSII as well as reactions linked to the photorespiratory cycle, including Rubisco in the chloroplast, glycolate oxidase, and CAT-peroxidase reactions in the peroxisome (Apel and Hirt 2004). When plants are subjected to environmental conditions that restrict the availability of CO_2 within the leaf, such as during drought or heat stress, the electron transfer chain (ETC) becomes saturated. The PSII complex transfers surplus electrons to diverse acceptors inside the chloroplast to avoid photoinhibition (Ort and Baker 2002). This is known as photochemical quenching, in which a portion of the electron is diverted to O_2, enabling $O_2^{\bullet-}$ to be formed at PSI via the Mehler reaction, which regeneration of NADP+. The $O_2^{\bullet-}$ generated at PSII is then dismutated to H_2O_2 in the thylakoid membrane, either spontaneously or by SOD enzyme. This efficient cycle mechanism shortens the lifetime of photoproduced $O_2^{\bullet-}$ and H_2O_2 to suppress the production of $^{\bullet}OH$ radicals, whose interaction with target molecules is thus prevented, leading to photoinhibition.

The thylakoid membrane generates $O_2^{\bullet -}$, which is unique to the chloroplast, by transferring energy from P680, the major electron donor at PSII, to ground O_2 (Asada 2006). Rubisco photorespiratory oxygenation of ribulose 1,5 bisphosphates are another electron sink in C_3 plants that helps prevent photoinactivation of PSII when CO_2 supply is limited. This mechanism maintains partial oxidation of PSII acceptors, and Rubisco catalyzes a competitive process in which oxygen is preferred as a substrate over CO_2 when temperature or intracellular CO_2 concentration rises (Apel and Hirt 2004). This oxygenation process results in the release of glycolate, which is then transported from chloroplasts to peroxisomes. The glycolate oxidase catalyzes the subsequent oxidation of glycolate, which accounts for the majority of the H_2O_2 generated during photosynthesis (Fig. 7.1).

7.2.1.2 Mitochondrial ROS Production

On a much smaller scale, mitochondria also produce damaging ROS (H_2O_2 and $O_2^{\bullet -}$). The mitochondrial electron transport chain (mETC), situated in the inner mitochondrial membrane, has enough energetic electrons to convert O_2 to $O_2^{\bullet -}$ (Bano et al. 2021). Complex I and Complex II are two major components of the mtETC that function as electron donor agents in the generation of ROS (Noctor et al. 2007). Complexes I and II create $O_2^{\bullet -}$ on the matrix side of the inner mitochondrial membrane. Because there are no significant changes between plant and animal complex III, it may be inferred that $O_2^{\bullet -}$ generation occurs on both sides of the inner mitochondrial membrane in plants (Fig. 7.2). Within the mitochondrial matrix $O_2^{\bullet -}$ is dismutated to H_2O_2 either spontaneously or by the mitochondrial manganese SOD. Because a complete set of enzymes required for the completion of the ascorbate-glutathione (ASC-GSH) cycle has been localized inside the plant's mitochondria, H_2O_2 is scavenged by the ascorbate peroxidase (APX). Mitochondria create ROS during respiration in general, but ROS production increases under stress circumstances, potentially leading to programmed cell death (Pastore et al. 2006) (Fig. 7.2).

7.2.1.3 Apoplastic ROS Production

Another source of ROS, particularly H_2O_2, is the apoplast. The apoplast is the diffusible region around the plant cell membrane that appears to be in charge of the exchange of nutrients and signals between plant cells and the environment, including the conversion of incoming CO_2 into a soluble, diffusible form that can be transported into the cytoplasm for photosynthesis (Bano et al. 2021). Many plant responses to external and endogenous stimuli include the buildup of ROS inside this compartment. In contrast to intracellular sources, apoplastic ROS generation is caused by active activation of ROS-producing enzymes such as apoplastic peroxidases, polyamine oxidases, and plasma membrane localized NADPH oxidases (respiratory burst oxidase homologs) (RBOHs) (Camejo et al. 2016). However, despite mounting evidence that apoplastic peroxidases are important, particularly in plant immunology, little is known about the molecular processes that govern the activity of these enzymes. NADPH oxidases are the most common type of apoplastic ROS generator (Choudhary et al. 2020). In order to produce $O_2^{\bullet -}$, electrons are

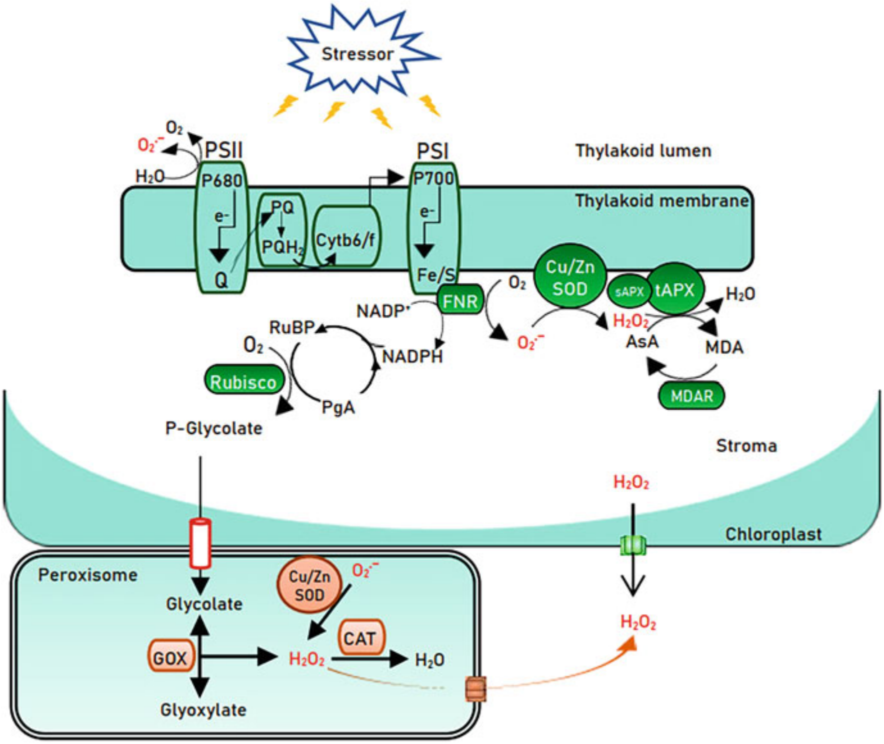

Fig. 7.1 A simplified model of reactive oxygen species generation in peroxisomes and chloroplasts via the photosynthetic electron transport chain. (Image courtesy of Microsoft Office). Ribulose-1,5 bisphosphate carboxylase-oxygenase (Rubisco), Ribulose 1-6-bisphosphate (GOX). (RUBP). Autoxidation of reduced ferredoxin at the photosystem I (PSI) and plastoquinone (PQ) levels in photosystem PSII produces superoxide anion ($O_2^{\bullet -}$), which is subsequently dismutated into hydrogen peroxide (H_2O_2) by the superoxide dismutase (SOD) enzyme. Electron (e^-), Ferredoxin-NADP reductase (FNR), Cytochrome b6f with 7 prosthetic groups (Cyt b6/7), Iron/Sulfur (Fe/S), monodehydroascorbate (MDA), water (H_2O), singlet oxygen ($^1O_2$), plastocyanin, photosystem I (PSI), photosystem II (PSII), nicotinamide adenine dinucleotide phosphate reduced and oxidized forms (NADPH/NADP+), photosystem II primary donors (p680/p700), thylakoid-bound ascorbate peroxidases (tAPX), plastoquinone (PQ), Stroma-bound ascorbate peroxidases (sAPX), Ribulose 1-6-bisphosphate (RUBP), monodehyroascorbate reductase (MDAR), glycolate oxidase (GOX), ascorbate (AsA), Ribulose-1,5 bisphosphate carboxylase-oxygenase (Rubisco)

transferred across the plasma membrane from cytoplasmic NADPH to molecular oxygen. The generated $O_2^{\bullet -}$ can be dismutated to H_2O_2 either naturally or by apoplastic SODs (Marino et al. 2012; Mittler 2017). Surprisingly, as compared to the intracellular environment, the apoplast is kept moderately oxidized and is thought to retain the majority of the leaf H_2O_2 despite containing modest quantities of ascorbate and reduced glutathione.

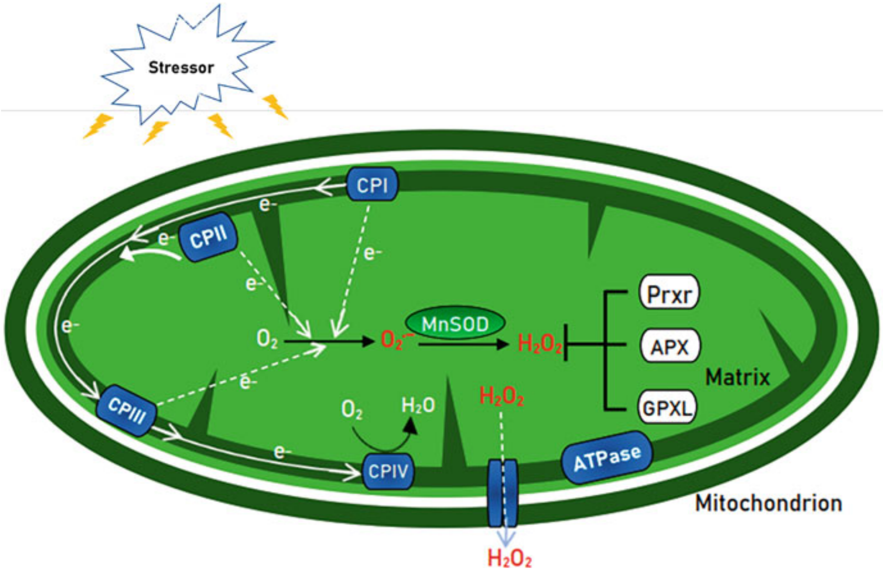

Fig. 7.2 Proposed model of ROS generation in the mitochondria, with plausible scavenging enzymes. boxes CPI–CPIV stand for complexes of the mETC I to IV. Electron (e^-), Ascorbate peroxidase (APX), Glutathione peroxidase-like (GPXL), manganese SOD (mnSODs), Peroxiredoxin (Prxr)

7.2.1.4 Plasma Membranes ROS Production

Plant cells are encircled by a cytoplasmic membrane that continually interacts with changing environmental environments, granting vital information for their survival. When electrons move from cytosolic NADPH to $O_2^{\bullet-}$, they are either dismutated spontaneously to H_2O_2 or catalyzed by NADPH oxidase. The role of NADPH oxidase in plant defense against pathogenic infection and abiotic stress conditions is well known (Eaton et al. 2008; Bano et al. 2021).

7.2.1.5 Cell Walls ROS Production

Lipoxygenase (LOX) is a cell wall-localized enzyme that hydroperoxidizes polyunsaturated fatty acids, which renders it an active ROS producer such as $OH^{\bullet}$, $O_2^{\bullet-}$, H_2O_2, and $^1O_2$. Cell wall-localized diamine oxidases generate ROS in the cell wall by utilizing diamines or polyamines. During the pathogenic onslaught, lignin precursors are cross-linked extensively via H_2O_2-mediated pathways, culminating in the synthesis of recombinant lignin (Higuchi 2006; Bano et al. 2021).

7.3 The ROS/Antioxidant Ratio Dictates the Cell Oxidative Status

Cellular homeostasis is dependent on the right equilibrium between ROS production and elimination at lower doses, ROS act as second messengers in intracellular signaling cascades, mediating plant responses such as stomatal closure and stress tolerance. Meanwhile, stressors such as salt, metal toxicity, and viruses upset the equilibrium, causing damages to biomolecules such as lipids, proteins, and DNA. Plant cells balance the formation of reactive oxygen species (ROS) and antioxidant enzymes to maintain redox equilibrium. A properly functioning defense system maintains a balance between ROS creation and elimination. It is essential for appropriate signaling to maintain an uninterrupted balance between ROS production and scavenging mechanisms. A disruption in the ROS/antioxidant balance can result in oxidative stress, which can cause permanent damage to nucleic acid, protein, carbohydrates, and lipid peroxidation, altering glucose metabolism and potentially leading to cell malfunction and death (Kuluev et al. 2019; Bano et al. 2021).

7.3.1 The Roles of ROS in Signaling Events

Depending on the plant's oxidative state, ROS can be classified as hazardous byproducts of aerobic metabolism or as crucial signal chemicals that tune metabolism and plant growth (Huchzermeyer et al. 2022). Essentially, ROS are produced in cell walls, cytoplasmic organelles, and plasma membranes, but they cause significant alterations in cellular processes. This suggests that the former operate as a second messenger in intracellular signaling cascades that control a number of plant responses (Eaton et al. 2008). ROS fine-tune gene expression at distances from the nucleus through three principal modes: activation of ROS-sensitive receptors, direct oxidization of signaling pathway components, and modulation of transcription factors. ROS affect protein kinases, phosphatases, transcription factors, undergo cross-talks with other signal molecules, affecting therefore major cell signaling pathways (Higuchi 2006; Eaton et al. 2008; Huchzermeyer et al. 2022).

7.3.2 ROS Activation of Mitogen-Activated Protein Kinase Signaling Pathway

Eukaryotic cells utilize the mitogen-activated protein kinase (MAPK) cascade for multiple signal transduction and activation of downstream cytoplasmic and nucleus components. The signaling process is initiated when MAPK kinase kinase (MAPKKK) activates MAPK kinase (MAPKK) which in turn, activates MAPKs, the final component that results in plant acclimation or reestablishment of cellular homeostasis. This signaling network is vital for cellular function given that it plays a role in converting ROS (second messenger) to protein phosphorylation/dephosphorylation, leading to the elicitation of cell reaction to stress, to cytokinesis and other phytohormones (Kaur et al. 2019). Several studies have comprehensively proven the causal relationship between the MAPK cascade and ROS. In this regard, Liu and He (2017) claimed that exogenous H_2O_2 administration promotes the activation of numerous components in the MAPK cascade by inactivating MAPK repressors. H_2O_2activates MAPKs, MPK3, and MPK6 in Arabidopsis through MAPKKK ANP1. Although neither the method of activation nor the downstream targets of the MAPK pathways are understood, ROS-induced MAPK activation appears to be essential in mediating cellular responses to a variety of stressors. A W-box and WRKY transcription factors, found in the tobacco RBOH gene's promoter region were both phosphorylated by MAPK (Liu and He 2017), demonstrating a crosstalk between RBOH and MAPK phosphorylation.

7.3.3 ROS Activate Some Transcription Factors (TFs)

To transmit ROS signals to specific transcription factors (TFs), plants and other eucaryotic cells have developed a number of systematically organized components, such as phosphatase, GTPase, lipase, as well as phospholipid-dependent and MAP kinases. Reactive cysteine thiol groups, whose redox state has been proven to be altered, are found in several ROS-regulated TFs (Kaur et al. 2019). Moreover, ROS control the activity of the transcription factors OxyR and Yap1 in *E. coli* by altering its cysteine thiol groups. Diverse ROS species are capable of activating several genes through the modification of cysteinyl residues the same transcription factor. Despite the aforementioned claims, there has been a growing interest in understanding how ROS target a specific TFs and control gene expression. However, research now available suggests that extremely intricate signaling networks including H_2O_2 and phytohormones like ABA, San, and JA are involved (Kaur et al. 2019). Presumably, in yeasts, animals, and plants the interaction of transcription factors with certain oxidative stress-sensitive cis-elements of the promoter sequences is suggested (Gasch et al. 2000; Apel and Hirt 2004). ROS can either directly regulate TFs or induce the expression of certain genes that influence the gene expression patterns of other signal transduction networks. Microarray analysis of H_2O_2-induced gene expression in Arabidopsis reveals possible H_2O_2-responsive cis-elements in H_2O_2-regulated genes (Desikan et al. 2001). Furthermore, up to 60 H_2O_2-responsive TFs were discovered as being engaged in the responses to cold, drought, heat, sunlight, and pathogens (Hieno et al. 2019). GSH, on the other hand, improves tomato tolerance to Cd stress by boosting the antioxidant system through redox-dependent activation of TFs such as the ethylene-responsive TFs ERF1, ERF2, and other stress-related genes (Hasan et al. 2016; Kaur et al. 2019).

7.3.4 ROS as Signals for Gene Expression

The de novo synthesized antioxidant chemicals (ASC-GSH cycle), which play a key role in controlling H_2O_2 concentrations in cells, maintain redox balance in stressed cells (Kaur et al. 2019). This clearly shows that redox imbalance mediates transcriptome modification in order to restore equilibrium. Recent advances in transcriptome analysis employing complete genome chips have revolutionized our understanding of gene expression. Environmental changes, such as an increase in H_2O_2, are claimed to alter 10% of the whole yeast transcriptome (Gasch et al. 2000; Chen et al. 2003). Furthermore, it has been demonstrated that almost 2% of tobacco genes, which largely involve in cellular defense, detoxification, and signal transduction, were elevated in acclimated leaves, showing a substantial alteration in a range of cellular responses during stress acclimation. In plants, ROS-induced genes have been identified for annexin (Moseyko et al. 2002; Apel and Hirt 2004), receptor kinase, and peroxisome biogenesis (Desikan et al. 2001), following exposure of Arabidopsis cells to H_2O_2. Recent OMIC approaches using cDNA microarrays techniques have enlarged the list of ROS-sensitive genes to those imply in organellar function, carbohydrate metabolism, protein folding and degradation, ROS detoxification, metabolite transport, plant growth, transcription, RNA processing, translation, nucleotide biosynthesis (Gasch et al. 2000; Chen et al. 2003; Apel and Hirt 2004). For instance, H_2O_2 signaling and accumulation has been shown to activate enzymatic antioxidant-encoding gene expression such as catalase (CAT), quinone reductase, glutathione peroxidase (GPX), SOD, thioredoxin reductase, and γ-glutamylcysteine synthase to withstand harsh environmental conditions (Kaur et al. 2019; Hwang and Chien 2022).

7.3.5 ROS in Cell-to-Cell Signaling

The above-described ROS-mediated signaling pathways are quite limited in the sense that they undergo signal ignition and transduction within a single cell. The so-called single-cell model do not adequately illustrate how ROS signals could affect the neighboring cells and eventually the whole plant (Miller et al. 2010). Of note, the redox state of apoplast marked by triggered accumulation of ROS and reduced antioxidant capacity during stress state cause faster diffusion of ROS (H_2O_2 for instance) in the apoplastic space, constituting potential second messengers of the redox state of the initial cell to the adjacent ones (Foyer and Noctor 2016). Hence, a self-propagating mechanism of cell-to-cell signaling via RBOHD-derived apoplastic ROS has been recently identified as a pivotal response to most of the ROS signaling mechanisms outlined above (Miller et al. 2010; Waszczak et al. 2018). Choi et al. (2014) discovered the ROS-activated tonoplastic channel TWO-PORE CHANNEL 1 (TPC1), which releases Ca^{2+} into the cytosol during stress, the microbes associated molecular pattern (MAMP) and ROS-induced phosphorylation of RBOHD via the Ca^{2+} sensor Calcium-Dependent Protein Kinase5 (CPK5). This clearly indicates that Ca^{2+} and ROS signals are coordinated via Ca^{2+}-dependent phosphorylation of NADPH oxidases (Steinhorst and Kudla 2014; Evans et al. 2016; Waszczak et al. 2018). The resulting $O_2^{\bullet -}$ enables message transmission from cell to cell. However, how do ROS signals in the apoplast reach and alter the cytosolic signaling components of neighboring cells, how do these initial compartment-specific

ROS-sensing and ROS signaling processes maintain specificity, and ultimately, how do ROS then link to downstream hormones are dark spots that need insights (Waszczak et al. 2018).

7.4 Redox-Based Damages to Biomolecules

7.4.1 Lipids Peroxidation

Lipids, particularly polyunsaturated fatty acids, are vulnerable to oxidative transformations caused by ROS. Increasing ROS level promotes lipid peroxidation in cell and organelle membranes, impairing normal cellular function. ROS-induced modifications, such as $^{\bullet}OH$ and $^{1}O_2$, are primarily generated in galactolipids and phospholipids, resulting in the formation of lipid hydroperoxides that disrupt membrane fluidity, increase permeability, and damage the proteins and DNA contained within them (Begara-Morales et al. 2021). Drought, salt, and heat stress, as well as any ROS-forming environmental factor, have all been found to induce lipid peroxidation in stressed cells. Radicals formed as a result of lipid peroxidation are employed as a biomarker for ROS-mediated membrane damage (Yadu et al. 2016).

7.4.2 Damages to Nucleotides and DNA

The hydroxyl radical ($^{\bullet}OH$) is one of the most damaging ROS to poly-nucleic acids due to its ability to change the pyrimidine and purine structure by releasing the proton (H^+) from the C-H bonds of the methyl and 2-deoxyribose groups, leading to the formation of deoxyribose radical, thymine glycol, hydroxyl methyl urea, and other compounds (Chmielowska-Bąk et al. 2019). These nitrogenous base changes cause base pairing errors, erroneous copies during replication, ribosomal blocking of translation, the production of truncated proteins with the resulting lack of function, and premature mRNA degradation (Simms et al. 2014; Chmielowska-Bąk et al. 2019; Sano et al. 2020; Katsuya-Gaviria et al. 2020). Furthermore, oxidations can alter the methylation pattern of cytosines implicated in gene expression control (Halliwell 2006). Subsequently, the plant growth, and development as well as functioning are altered such as susceptibility to diseases and abiotic stressors, reduced photosynthesis as well as other cell vital functions which may lead to cell death (Bano et al. 2021).

7.4.3 Damage to Carbohydrates

Some ROS, particularly those containing hydroxyl groups $^{\bullet}OH$, have been shown to react with free carbohydrates such as sugars and polyols, as well as structural cell wall polysaccharides. Its reaction with free sugars such as mannitol results in an antioxidant defense response that prevents the OH reaction with more critical cellular macromolecules, hence avoiding superior oxidative damage (Møller et al. 2007). However, high oxidative stress conditions indirectly stimulate autoxidation of monosaccharides, resulting in the synthesis of dicarbonyls, particularly methyl glyoxal, glyoxal, and 3-deoxy glucosone. These chemically reactive substances can alter Arg and Lys residues in proteins, resulting in glycation, a PTM associated with enzyme deactivation (Chaplin et al. 2019; Rabbani et al. 2020; Matamoros and Becana 2021).

7.4.4 Damage to Proteins

ROS assaults on amino acids, peptides, and proteins can be done in a variety of ways. The former directly cause protein damage by altering protein function via, carbonylation, disulfide bond formation, glutathionylation, and nitrosylation. ROS also damage proteins indirectly via fatty acid peroxidation products (Møller and Kristensen 2004). The primary targets are the 20 proteinogenic amino acids, which differ in their chemical reactivity and sensitivity to damage (changes) as well as their ability to host post-transcriptional modification (PTM). Among these amino acids, those containing sulfur, particularly those with reactive thiol groups, stand out: cysteine and methionine (Waszczak et al. 2015; Akter et al. 2015). The subsequent alteration of amino acid residues affects enzyme active sites, breaks peptide chains, aggravates cross-linked reactions, changes protein net charge, and boosts proteolytic activity. The sensitivity to sulfur-containing amino acids is substantially lower, therefore their modification will be determined by their interactions with more unstable reactive oxygen species, a conducive microenvironment, as well as its Pka (Ehrenshaft et al. 2015; Matamoros and Becana 2021).

7.5 ROS Detoxification Mechanisms

To protect themselves from the above-mentioned oxidative stress-induced damages, plants employ a complex of antioxidant defense machinery. These antioxidants are present in plant cells and different organelles such as mitochondria, chloroplast, and peroxisomes, and are grouped as non-enzymatic and enzymatic antioxidants (Mittler et al. 2004; Sharma et al. 2022).

7.5.1 Non-enzymatic ROS Scavenging Mechanisms

Antioxidants such as ascorbic acid (ASH); glutathione (GSH); a-tocopherols, carotenoids, phenolic compounds, and proline are non-enzymatic components of ROS scavenging machinery (Gill and Tuteja 2010; Abdulfatah 2022). In addition to their roles in defense and as enzyme cofactors, these components play an important role in plant growth by slowing down cellular processes such mitosis, cell elongation, senescence, and plant death (de Pinto 2004).

7.5.2 Ascorbic Acid (ASH)

ASH or ascorbate is the most occurrent, low molecular weight, powerful, water mixable antioxidant which prevent or minimize ROS damages (Smirnoff 2005; Bilska et al. 2019). ASH is located in the cytoplasm (90%) although substantial portions is found in apoplast. Apoplastic ASH constitute the first defense line to external reactive oxygen species attack (Barnes et al. 2002). The chloroplast contains around 30–40% of the total ASH were it is present in reduced form (Sandalio and Del Río 1988; Smirnoff 2005). Because of his ability to provide electrons in a variety of enzymatic and non-enzymatic activities, ASH is recognized as a particularly effective ROS scavenger. It reacts with H_2O_2, $^{\bullet}OH$, and $O_2^{\bullet-}$ and gets transformed into an alpha-tocopherol from tocopheroxyl radicals. in turn, the stabilization of these ROS protects membranes from oxidative damage and preserves the activity of biomelecules (Seminario et al. 2017). High light intensity, UV-B radiation, drought, and other stressors have been shown to significantly enhance ASH in plants (Agarwal 2007; Yang et al. 2008).

7.5.3 Glutathione (GSH)

Glutathione (-glutamyl cysteinyl-glycine) is a critical low molecular weight thiol tripeptide present in plant tissues in reduced form (GSH). It is synthesized in plant cells' cytosol and chloroplasts and found in practically all cell compartments and organelles (Foyer and Noctor 2003; Srivalli and Khanna-Chopra 2008). Furthermore, GSH interacts with H_2O_2, $^1O_2$, $^{\bullet}OH$, and $O^{\bullet}$ or works directly as a free radical scavenger. GSH may also form adducts (glutathiolated) with reactive electrophiles to preserve macromolecules (proteins, lipids, DNA) or decrease biomolecules in the presence of ROS or organic free radicals to generate GSSG (Das and Roychoudhury 2014; Foyer 2019).

7.5.4 α-Tocopherol (Vitamin E)

Tocopherols are lipophilic antioxidants found in plant chloroplast thylakoid membranes. Tocopherols scavenge ROS such as oxygen free radicals, lipid peroxyl radicals, and $^1O_2$ (Quadrana et al. 2013). They are known to preserve lipids and other membrane components by blocking the chain propagation phase in the lipid auto-oxidation cycle, as well as by reacting with O_2 and quenching its excess energy, hence safeguarding PSII structure and function (Ivanov and Khorobrykh 2003). Because of its three methyl substituents, the -tocopherol isoform is the most active, important defender, and vital component of biological membranes. At the membrane-water contact, -tocopherol lowers the lipid radicals $RO^{\bullet}$, $ROO^{\bullet}$, and $RO^{\bullet}$ and transforms itself to $TOH^{\bullet}$.

7.5.5 Carotenoids

Carotenoids are pigments present in both plants and microorganisms (Gill and Tuteja 2010). They are found in the plastids of both photosynthetic and non-photosynthetic plant tissues in plants (Das and Roychoudhury 2014). Nature has about 600 different carotenoids. They perform a variety of functions that are classified into three groups. (1) light harvesting: they absorb light in the visible spectrum between 400 and 570 nm and transfer the energy to the chlorophyll molecule; (2) antioxidant function: they protect the photosynthetic apparatus by quenching triplet sensitizer (3Chl) and excited chlorophyll (Chl^*) molecules to prevent $^1O_2$ formation. (3) Structural function: crucial for thylakoid membrane and light harvesting complex protein stability, as well as PSI assembly (Gill and Tuteja 2010; Pospíšil 2012; Das and Roychoudhury 2014). Furthermore, carotenoids are signaling molecule precursors that influence plant response to biotic and abiotic stressors, as well as plant growth (Li et al. 2008).

7.5.6 Phenolic Compounds

Polyphenols are secondary metabolites found in abundance and diversity in plant tissues (Grace and Logan 2000). They have an aromatic group that is replaced by –OH or O-CH3, and they interact together for biological functions as antioxidants. Polyphenols can inhibit the spread of free radicals and restrict peroxidase reactions by scavenging ROS and suppressing lipid peroxidation (LPO) (Arora et al. 2000; Sharma et al. 2012). Among the most bioactive polyphenols are flavonoids. Furthermore, flavonoids are thought to be secondary ROS scavengers, neutralizing free radicals to protect cells (Løvdal et al. 2010; Fini et al. 2011). Flavonols are among the most common flavonoids in plants, and they are thought to be excellent UV filters due to their capacity to concentrate in glycosylated form after light treatment and absorb UV-B radiation in the 280–320 nm range (Solovchenko 2003).

7.5.7 Proline (Pro)

Proline is not only an osmolyte but also an antioxidant that is biosynthesized in the chloroplasts, mitochondria, and cytosol of all plants as well as algae under stressful circumstances (Verbruggen and Hermans 2008). Proline is frequently employed as a non-enzymatic antioxidant by microorganisms, animals, and plants to prevent the detrimental effects of ROS (Chen and Dickman 2005). Under abiotic stress, high proline accumulation may be linked with enhanced synthesis or reduced degradation. Free proline is an effective $OH^•$ and $^1O_2$ scavenger as well as an LPO inhibitor, osmoprotectant (Table 7.1), protein stabilizer, and metal chelator (Ashraf and Foolad 2007; Verbruggen and Hermans 2008; Trovato et al. 2008). Overexpression of genes in the Pro biosynthesis pathway promotes abiotic stress tolerance in transgenic plants, according to research. In addition, the ability of proline to scavenge ROS

Table 7.1 Cellular localization and mode of action of some cellular non-enzymatic ROS scavengers

Antioxidant	Sub-cellular localization	Mode of action on ROS
Ascorbic acid (ASH)	Cytoplasm, apoplast, chloroplast, mitochondria, peroxisome, and vacuole	Scavenges H_2O_2, OH•, $O_2^{\bullet-}$ and produce α-tocopherol
Glutathione (GSH)	Cytosol, chloroplast, endoplasmic reticulum, mitochondria, peroxisome, vacuole, and apoplast	Scavenges free radicals, forms adduct with reactive electrophiles, acts as a detoxifying co-substrate for enzymes like peroxidases, GR and GST
α-tocopherol (Vit. E)	Thylakoid membrane of chloroplasts	Scavenges ROS like oxygen free radicals, $^1O_2$ and lipid peroxyl radicals like $RO^{\bullet}$, $ROO^{\bullet}$ and RO^*
Carotenoids	Plastids of photosynthetic and non-photosynthetic plant tissues	Quenches triplet sensitizer ($3Chl^*$) and excited chlorophyll (Chl^*), acts on $^1O_2$
Phenolic compounds	Vacuole	scavenges ROS like H_2O_2, $OH^{\bullet}$, $O_2^{\bullet-}$ and suppress lipid peroxidation (LPO)
Proline	Mitochondria, cytosol, and chloroplast	scavenges $OH^{\bullet}$, $^1O_2$ and inhibit LPO

Reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2), hydroxyl radical ($OH^{\bullet}$), superoxide anion ($O_2^{\bullet-}$), singlet oxygen ($^1O_2$), peroxyl radical ($ROO^{\bullet}$), alcoxyl radical ($RO^{\bullet}$), excited alkoxyl group (RO^*), suppressing lipid peroxidation (LPO), quenching excited chlorophyll (Chl^*) as carotenoids or act as co-substrate for enzymes such as peroxidases, glutathione reductase (GR), and glutathione-*S*-transferase (GST)

or prevent ROS-mediated apoptosis was identified as a crucial function in response to cellular stress (Gill and Tuteja 2010).

7.5.8 Enzymatic ROS Scavenging Mechanisms

The enzymatic ROS scavengers are mainly catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), guaiacol peroxidase (GPOX), glutathione peroxidase (GPX), and glutathione reductase (GR) (Gill and Tuteja 2010**).**

7.5.9 Superoxide Dismutase (E.C.1.15.1.1)

SOD (superoxide dismutase) is a metalloenzyme that is the most potent intracellular enzymatic antioxidant in aerobic organisms (Mittler et al. 2004). SOD is found in nearly all sub-cellular compartments where ROS are produced and serves as the first line of defense against oxidative damage. SOD removes $O_2^{\bullet-}$ by catalyzing its dismutation to O_2 and H_2O_2, lowering the potential of $^{\bullet}OH$ production via the metal-catalyzed Habere-Weiss reaction. This reaction is 10,000 times quicker than natural dismutation. Based on their metal cofactors, three SOD isozymes have been identified: Mn-SOD, found in mitochondria; Fe-SOD, found in chloroplasts when present; and Cu/Zn-SOD, found in cytosol, peroxisomes, and chloroplasts (Bagnoli et al. 2001; Nandini and Samir 2016) Many studies have found that plants subjected to environmental conditions have an increase in SOD levels (Harinasut et al. 2003; Boguszewska et al. 2010). As a result, SOD might be utilized as an indirect criteria for the selection of drought-tolerant plants (Zaefyzadeh et al. 2009).

7.5.10 Catalase (E.C.1.11.1.6)

Catalase (CAT) was the first antioxidant enzyme to be found and studied. It is a heme-containing tetrameric enzyme that catalyzes the dismutation of two molecules of H_2O_2 into H_2O and $O_2^{\bullet -}$. AT is highly selective for H_2O_2 and has a lower affinity for organic peroxides. It has an extremely quick turnover rate, as one molecule of CAT can convert 6106 molecules of H_2O_2 per minute to H_2O and O_2. It is a unique antioxidant since it does not require a cellular reducing counterpart to function. It is primarily produced in Peroxisomes as a result of photorespiratory oxidation, fatty acid oxidation, purine catabolism, and oxidative stress (Mittler 2002; Corpas et al. 2008; Garg and Manchanda 2009). This change in activity was observed under Cd stress in *A. thaliana* (Cho and Seo 2005), *Capsicum annuum* (León et al. 2002), and *Glycine max* (Balestrasse et al. 2001), whereas *Triticum aestivum* (Khan et al. 2007), *C. arietinum* (Hasan et al. 2008), and *V. mungo* roots (Singh et al. 2008). However, stress-induced protein depletion is often linked with decreased CAT activity. Aside from H_2O_2, CAT may also react with hydroperoxides such as methyl hydrogen peroxide (MeOOH) (Ali and Alqurainy 2006).

7.5.11 Ascorbate Peroxidase (E.C.1.1.11.1)

Ascorbate peroxidase (APX) is a required enzyme in the Ascorbate-Glutathione (ASC-GSH) cycle. It is in charge of converting H_2O_2 to water and DHA in the cytosol and chloroplast (Welinder 1992; Das and Roychoudhury 2014). There are five isoenzymes classified based on amino acid sequences and location, including thylakoid (tAPX) and glyoxisome membrane forms (gmAPX), as well as chloroplast stromal soluble form (sAPX) and cytosolic form (cAPX) (Noctor and Foyer 1998; Sharma and Dubey 2004). Under stressed conditions, APX is the most effective H_2O_2 scavenger due to his stronger affinity for H_2O_2. It is one among the most abundant antioxidant enzymes in plants (Wang et al. 1999). Drought, salinity, metal toxicity, cold, and UV irradiation all enhance the activity of APX (Han et al. 2009). Overproduction of the enzyme increases the activity of peroxidase (POD), which is responsible for the activation of the ROS scavenging system in plants, resulting in stress tolerance and disease resistance (Sarowar et al. 2005).

7.5.12 Monodehydroascorbate Reductase (E.C.1.6.5.4)

The reaction catalyzed by APX produces MDHA (Monodehydroascorbate), a short-lived enzyme that rapidly creates ascorbate (AA) and dehydroascorbate (DHA) (Ushimaru et al. 1997; Mittler 2002). MDHAR is a flavin-adenine dinucleotide (FAD) enzyme that regenerates AA from MDHA by preferring NADH over NADPH as an electron donor. MDHAR contains numerous isoenzymes that are found in peroxisomes, chloroplasts, cytosol, and mitochondria. It is also recognized as the sole enzyme that uses organic radical (MDA) as a substrate (Dalton et al. 1993; Jimenez et al. 1997). Chloroplastic MDHAR may have two physiological roles, including the regeneration of AA from MDHA and the photoreduction of dioxygen to $O_2^{\bullet -}$. Multiple investigations have shown that under environmental stress circumstances, MDHAR activity increases (Miyake et al. 1998).

7.5.13 Dehydroascorbate Reductase (EC 1.8.5.1)

Dehydroascorbate reductase (DHAR) keeps ascorbate (AA) in the reduced form by catalyzing the reduction of DHA to ASH using GSH as an electron donor (Ushimaru et al. 1997; Eltayeb et al. 2007). It is a component of the Ascorbate-Glutathione (ASC-GSH) cycle, which is critical for controlling the amount of the AA pool in symplast and apoplast (Chen and Gallie 2006). Several studies have shown that certain environmental stressors boost DHAR activity. Yin et al. (2010) found that DHAR overexpression causes tolerance to Al stress by boosting AA levels. Overexpression of the enzyme also protected tobacco plants from ozone and drought stress and improved salt tolerance in Arabidopsis (Eltayeb et al. 2006; Chen and Gallie 2006; Ushimaru et al. 2006).

7.5.14 Glutathione Reductase (EC 1.6.4.2)

Glutathione reductase (GR) is a flavoprotein oxidoreductase, catalyzing the reduction of glutathione disulfide (GSSG), oxidized glutathione to GSH, reduced glutathione using NADPH as reductant (Madhava Rao et al. 2006; Khan et al. 2008; Das and Roychoudhury 2014). The GSSG is composed by two GSH linked by a disulfide bridge and the generated reduced glutathione (GSH) upon the action of GR, is involved in many metabolic regulatory and antioxidative processes in plants (Ghisla and Massey 1989; Madhava Rao et al. 2006). It is an important enzyme of the ASH-GSH cycle. GR is predominantly found in chloroplasts (representing 80% of GR activity) but small amount can also be found in cytosol, mitochondria, and peroxisomes (Edwards et al. 1990). GSH and GR work in chloroplasts to detoxify the H_2O_2 generated by the Mehler reaction and play a key role in regulating plant tolerance to abiotic stress. GSH prevents thiol group oxidation and reacts with damaging ROS members such as $^1O_2$ and $^{\bullet}OH$ (Das and Roychoudhury 2014). Otherwise, Srivastava et al. (2005), Pastori and Trippi (1992), and Das and

Roychoudhury (2014) reported a direct correlation between resistance to oxidative stress and the activity of GR and elucidated a stimulation of GR de novo synthesis by oxidative stress caused by paraquat or H_2O_2. Overall, the antioxidant role of GR in plant was demonstrated ascribed to its ability to regenerate GSH and maintain the cellular AA pool (Ding et al. 2009).

7.5.15 Guaiacol Peroxidase (E.C.1.11.1.7)

Guaiacol peroxidase (GPOX) is an enzyme containing heme with 40–50 kDa monomers. GPOX plays many roles as consuming H_2O_2 during normal metabolism and under oxidative stress. It is also implicated in the synthesis of lignin and the degradation of indole-3-acetic acid (IAA). It is regarded as a key enzyme in the removal of H_2O_2 due to its presence and activity either in the intracellular (cytosol, vacuole), cell wall or extracellular compartments. Abiotic stress is recognized to increase the GPOX activity. In fact, under salinity stress, increase in GPOX activity was reported in leaf and root tissues of *Vigna radiate* (Yamane et al. 2009) and *O. sativa* (Panda 2001). Also, increase in GPOX activity under cadmium (Cd) stress and decrease after treatment were reported in spruce needles (Radotić et al. 2000).

7.5.16 Glutathione Peroxidase (EC 1.11.1.9)

Glutathione peroxidase (GPX) is an antioxidant enzyme utilizing GSH to reduce H_2O_2, organic and lipid hydroperoxides (Noctor et al. 2002). It is a large isoenzyme family found in chloroplasts, cytoplasm, mitochondria, and the endoplasmic reticulum. GPX has been demonstrated to induce plant tolerance to oxidative stress (León et al. 2002). Under stress scenarios, GPX activity increased in *C. annuum* plants, but Cd stress decreased enzyme activity in *P. sativum* plants (Dixit et al. 2001). Overexpression of GPX in transgenic plants has been shown to increase abiotic stress tolerance (Gill and Tuteja 2010). In *Chlamydomonas reinhardtii* subjected to oxidative stress (Table 7.2), a GPX homologue gene (Gpxh gene) was shown to be upregulated (Leisinger et al. 2001).

7.6 Melatonin, a Novel Multifaceted Cellular Antioxidant

7.6.1 Overview of Melatonin Biosynthesis

N-acetyl-5-methoxytryptamine known as melatonin (MET) is a ubiquitous molecule with low molecular weight and stable structure, firstly discovered in animals but later studies confirmed his presence in higher plants (Kanwar et al. 2018). Melatonin is present in different plant parts as fruits and seeds, flower buds, petals, leaves, stems, and roots of several plant species such as corn, rice, wheat, tobacco, barley, oat, grass, carrot, apple, cherry, and cucumber (Shibaeva et al. 2018; Tripathi et al. 2021;

Table 7.2 Cellular localization and mode of action of some cellular enzymatic ROS scavengers

Antioxidant	Sub-cellular localization	Mode of action on ROS
Superoxide dismutase (SOD)	Mitochondria, cytosol, peroxisomes, and chloroplast	Catalyzes dismutation of $O_2^{\bullet -}$ into O_2 and $H_2O_2^{\bullet -} + O_2^{\bullet}$ $^{-} + 2H^+ \rightarrow 2H_2O_2 + O_2$
Catalase (CAT)	Peroxisomes and mitochondria	Catalyzes the dismutation of two molecules of H_2O_2 into H_2O and O_2. $2H_2O_2 \rightarrow H_2O + 1/2O_2$
Ascorbate peroxidase (APX)	Cytosol, chloroplast and also peroxisomes and mitochondria	Reduces H_2O_2 to H_2O and DHA $H_2O_2 + AA \rightarrow 2H_2O + DHA$
Monodehydroascorbate reductase (MDAPX)	Peroxisomes, chloroplasts, cytosol and mitochondria	Regeneration of AA from MDHA and photoreduction of dioxygen to $O_2^{\bullet -}$ MDHA + NAD (P)H → AA + NAD(P)+
Dehydroascorbate reductase	Mitochondria, cytoplasm, and chloroplast	Reduces DHA to AA using GSH DHA + 2GSH → AA + GSSG
Glutathione reductase (GSH)	Chloroplasts (principally), cytosol, mitochondria, and peroxisomes	Reduces GSSG to GSH using NADPH GSSG + NAD (P)H → 2GSH + NAD(P)+
Guaiacol peroxidase (GPOX)	Mitochondria, cytoplasm, chloroplast, vacuole and endoplasmic reticulum,	Reduces H_2O_2 to H_2O using GSH $H_2O_2 + GSH \rightarrow H_2O + GSSG$
Glutathione peroxidase (GPOX)	Chloroplast, mitochondria, cytosol and endoplasmic reticulum	Reduces H_2O_2, organic and lipid hydroperoxides, using GSH $H_2O_2 + GSH \rightarrow H_2O + GSSG$

Enzymatic antioxidants are distributed in almost all aerobic cells and extracellular fluids. They are responsible for the dismutation of free radicals such as hydrogen peroxide (H_2O_2) and superoxide anion ($O_2^{\bullet -}$) into water (H_2O) and oxygen (O_2). Also involved in the Ascorbate-Glutathione (ASC-GSH) cycle, reacting with molecules like Monodehydroascorbate (MDHA), Dehydroascorbate (DHA), reduced glutathione (GSH), Ascorbate (AA), oxidized glutathione (GSSG) using NADPH (Nicotinamide adenine dinucleotide phosphate) as cofactor

Arnao and Hernández-Ruiz 2021). The biosynthesis of melatonin using tryptophan as precursor takes place in mitochondria and chloroplast although it can also be synthesized in the cytosol. In plants, the most abundant MET derivative is the 2-hydroxymelatonin (2-OHMET), and its intracellular concentration is twofold higher than the MET concentration (Byeon et al. 2015). This derivative is recognized as most active than the MET in the induction of stress tolerance in plant (Lee and Back 2016a). Six biosynthetic enzymes are involved including caffeic acid *O*-methyltransferase (COMT), *N*-acetyl serotonin methyltransferase (ASMT), serotonin-*N*-acetyltransferase (SNAT), tryptamine 5-hydroxylase (T5H), tryptophan hydroxylase, and tryptophan decarboxylase (TDC) (Sun et al. 2021). The TDC catalysis the decarboxylation of tryptophan into tryptamine which is hydroxylated by T5H to serotonin then SNAT and ASMT/COMT catalyze the final steps, respectively, for the production of *N*-acetyl serotonin and melatonin (Zhang et al. 2015)

(Fig. 7.3). MET is produced by a variety of bacterial species (taxa) such as cyanobacteria (production in chloroplasts) and a-proteobacteria (in mitochondria). Upon production, it is transported through the xylem to other plant parts and the activity is triggered by the receptor (CAND2/PMTR1) for stress response (Ayyaz et al. 2022).

7.6.2 ROS Scavenging Ability of Melatonin

Under normal conditions, MET level is constant while detrimental conditions such as cold, heat, salt, drought, radiation, oxidative, nutrient stress, and bacterial infection, directly stimulate its synthesis and accumulation (Zhang et al. 2015; Ma et al. 2017). MET protect plants against these stresses by regulating the enzymatic and non-enzymatic defense systems. It may serve as a ROS level regulator, either directly by scavenging ROS or indirectly by inducing redox enzymes that detoxify ROS, such as APX, CAT, POD, GPX, and SOD (Khan et al. 2020). Direct action consists in improving plant tolerance to diverse stressors by scavenging $O_2^{\bullet -}$, $^{\bullet}OH$, and other oxidative agents (Zeng et al. 2022). Non-enzymatic antioxidant agents such as GSH and ASH (Li et al. 2019; Ahammed et al. 2019), phenolic compounds (Dawood and Sadak 2014), flavonoid (Kim et al. 2010), and carotenoids (Sharma et al. 2020) are also mediated via MET. Furthermore, MET revealed the ability to restore endogenous antioxidants such as glutathione, vitamins C and E, as well as boost antioxidant defense systems (Zhang et al. 2015). In some studies, one molecule of melatonin may scavenge ten free radicals, which is more than the effectiveness of several antioxidant enzymes (Ye et al. 2016). Exogenous melatonin can induce the biosynthesis of endogenous own to boost protection of cell membrane and improve photosynthesis (Zhang et al. 2013; Imran et al. 2021; Chen et al. 2021). Furthermore, MET regulates the expression of several genes (Byeon et al. 2013; Zhang et al. 2014). For instance, when stressors are detected by receptors on the cell membrane, the signal is transduced and secondary messengers such as calcium and ROS are produced. Therefore, MET inhibit the expression of genes implicated along the signal transduction process. The molecule also down-regulated the expression of the light-regulated enzyme, chlorophyllase (CLH1) implicated in chlorophyll degradation (Weeda et al. 2014).

7.7 Interplay of Melatonin with ROS for Plant Stress Mitigation

Melatonin is a versatile chemical that protects plants from biotic and abiotic stressors (Zhang et al. 2022a). MET also interacts with other signal molecules such as ROS, nitric oxide (NO), and hydrogen sulfide (H_2S) to increase plant tolerance toward the stressor (Sun et al. 2021; Su et al. 2021; Gu et al. 2021; Zhang et al. 2022a; Arnao et al. 2022). Indeed, nitric oxide (NO) is a gasotransmitter that regulates plant growth and mediates stress tolerance by improving the antioxidant system (Siddiqui et al. 2011). Because of its strong capacity to diffuse across cellular membranes without

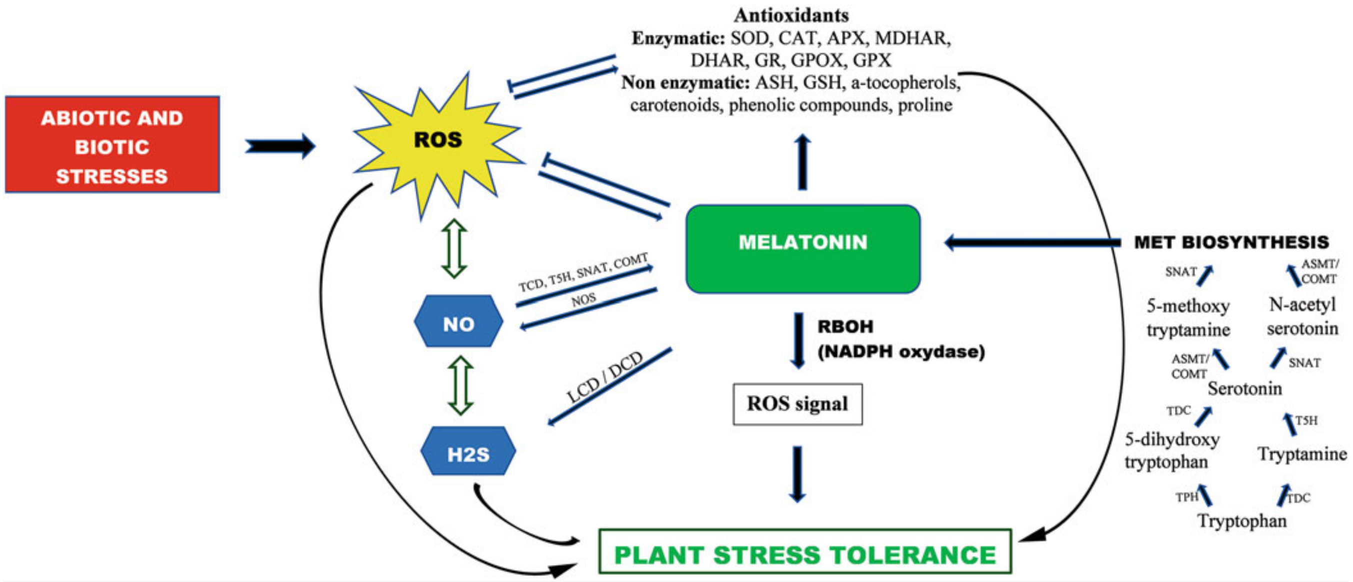

Fig. 7.3 Melatonine biosynthesis and mechanism to induce plant tolerance to stress as interaction with other signaling molecules, such as reactive oxygen species (ROS), nitric oxide (NO), and hydrogen sulfide (H_2S). (Picture credit; BioRender). CAT (catalase), SOD (superoxide dismutase), MDHAR (monodehydroascorbate reductase), APX (ascorbate peroxidase), GR (glutathione reductase), DHAR (dehydroascorbate reductase), GPX (glutathione peroxidase), GPOX (guaiacol peroxidase), GSH (reduced glutathione), ASH (ascorbic acid); RBOH (The respiratory burst oxidase homolog), SNAT (serotonin-*N*-acetyltransferase), T5H (tryptamine 5-hydroxylase), TDC (tryptophan decarboxylase), and COMT (caffeic acid *O*-methyltransferase) and ASMT (*N*-acetyl serotonin methyltransferase)

the usage of a specialized transporter, NO is a potent signaling molecule (Fancy et al. 2017). The antioxidant and ROS effects of MET and NO are dependent on their intracellular levels (Aydogan et al. 2006; Mur et al. 2013). Furthermore, NO can be synthesized by different oxidative and reductive pathways including oxidation of L-arginine by NO synthase, of polyamine, by polyamine oxidase, NADH/NADPH due to the action of cytochrome oxidase or reduction of NO_3^- to NO_2^- by nitrate reductase, followed by NO_2^- reduction to NO by xanthine oxidoreductase, and plasma-membrane-bound nitrite-NO reductase. In settings such as high nitrate concentrations or strongly reducing environments, nitrite may also generate NO (Gupta and Igamberdiev 2011; Santolini et al. 2017). Owing to its relatively short half-life (30 s), NO requires carriers such as *S*-nitrosothiols, which are more stable and act for NO transport and accumulation in plants (Berchner-Pfannschmidt et al. 2008). NO, once formed, can interact with other redox-related compounds and affect protein activity via several methods (Fancy et al. 2017). However, MET can increase stress tolerance by acting on NO, either by stimulating its synthesis or scavenging excess NO, or by increasing NO buildup via the arginine route. It can also upregulate NOS-related genes by boosting NOS activity and, as a result, NO levels (Liu et al. 2019; Aghdam et al. 2019). Furthermore, NO nitrosation utilizing oxygen and varied pH conditions can convert MET to *N*-Nitrosomelatonin (NOMET), while in cell cultures NOMET is an efficient NO donor. NO, on the other hand, can boost MET levels by promoting the expression of genes encoding enzymes involved in the MET biosynthesis pathway (TDC, T5H, SNAT, and COMT) (He and He 2020). Indeed, multiple studies have demonstrated the role of NO as a downstream signal in MET-mediated plant tolerance to abiotic stress. For example, MET improved rapeseed and sunflower seedling resistance to salt stress via NO signaling (Arora and Bhatla 2017; Zhao et al. 2018; Wang et al. 2021b). The interaction of NO and MET for plant response to unfavorable circumstances is intricated, since they interact separately and via numerous signaling pathways (Zhu et al. 2019).

Hydrogen sulfide (H_2S) is a colorless, flammable, and hydro-soluble gas that was once thought to be a poisonous molecule but is now thought to be the third endogenous gaseous transmitter after nitric oxide (NO) and carbon monoxide (CO) (Calderwood and Kopriva 2014; Zhang et al. 2021). H_2S is essential for plant growth and senescence, and it improves plant tolerance to a variety of biotic and abiotic stimuli (Huang et al. 2021). H_2S has also been shown to promote persulfidation, a reversible oxidative posttranslational alteration of protein cysteine residues that affects the redox function and status of targeted proteins (Zhang et al. 2022a). H_2S is commonly regarded as a gaseous signaling molecule that may interact with other signaling molecules such as melatonin (MET) via affecting gene expression and hence enzyme activity (Wang et al. 2021a). A range of enzymes, including cysteine synthase (CS), L-cysteine desulfhydrase (LCD), D-cysteine desulfhydrase (DCD), -cyanoalanine synthase (CAS), and sulfite reductase (SiR), can biosynthesize H_2S in the mitochondria, cytosol, and chloroplast (Papenbrock et al. 2007). As a result, MET can promote H_2S generation and accumulation by increasing the activities of LCD and DCD (Mukherjee and Bhatla 2021). Numerous studies have demonstrated the role of H_2S as a signal molecule on MET-mediated abiotic stress mitigation. Furthermore, in association with NO, H_2S enhance the activity of melatonin in inducing salinity tolerance in cucumbers and resistance to iron deficiency and salinity stress in pepper seedlings (Kaya et al. 2019; Sun et al. 2021).

Reactive oxygen species (ROS) have been widely described for their harmful effect on plants, where excessive accumulation cause oxidative stress and cell injury in severe cases. Therefore, they are also known for their positive effects on plants at moderate concentrations (Choudhury et al. 2017; Chen and Yang 2020). ROS are very important signal molecules mediating plant growth, development, and defense against external stresses. The high membrane permeability makes ROS perfect signals for the regulation of plants reactions (Sagi et al. 2004). Numerous studies revealed the role of MET on ROS production in order to induce plants tolerance to environmental stresses. For instance, MET stimulate H_2O_2 accumulation in watermelon in response to cold stress (Chang et al. 2021). Similarly, exogenous treatment with MET inhibits the stomatal closure and protect the photosynthesis apparatus of watermelon seedlings under salinity stress (Zhou et al. 2016). It was shown that in rice, MET induce ROS burst to reduce K^+ retention by enhanced expression of K^+ uptake transporters (Liu et al. 2020). The protective effects of MET on drought, cold and heat stresses in tomato was negatively affected by H_2O_2 scavengers (Gong et al. 2017). These reports evidently proved that ROS are important signal molecules for the activation of melatonin- regulated tolerance to abiotic stresses in plants.

7.8 Crosstalk Between ROS and Melatonin: The Role of the Respiratory Burst Oxidase Homolog (RBOH)

A plethora of signal molecules participate in the melatonin-ROS crosstalk, such as ROS. The former being widely distributed in plant cells. The NADPH oxidases, also known as RBOH, are the principal source of ROS generation in the apoplast. The RBOH is found on the plasma membrane and has a FAD/NADP(H)-binding domain at the C-terminus, a regulatory domain at the N terminus, six transmembrane domains, and numerous possible phosphorylation sites (Sagi and Fluhr 2006). In addition to this basic structure, the RBOH N terminus domain has a cytoplasmic expand of around 300 amino acids. This region has two conserved EF-hand structures where Ca^{2+} can be bound and strongly regulates oxidase activity (Foreman et al. 2003). In the apoplast, RBOH transfers electrons to O_2 molecules to generate $O_2^{\bullet -}$, which is then transformed into H_2O_2 either spontaneously or by the action of SOD, which detoxifies superoxide anion to hydrogen peroxide via an enzymatic process (Suzuki et al. 2011; Waszczak et al. 2018). Gong et al. (2017) found that MET lowers S-nitrosylation of RBOH, which activates the ROS signaling pathway and induces plant tolerance to abiotic stress. In Arabidopsis, MET has a transmembrane receptor called PMTR1/CAND2, which is also present in the plasma membrane and may activate RBOH by interacting with G-protein subunits, resulting in stomatal closure. This receptor has been identified in lucerne, maize, tobacco, and Arabidopsis (Wei et al. 2018; Kong et al. 2021; Wang et al. 2022). Because of the ease of application of molecular genetic methods, the Arabidopsis plant model is most commonly employed to describe the RBOH gene family. Ten RBOH genes (AtRbohA to AtRbohJ) in the plant encode NADPH oxidase. The signaling pathways, comprising reactive species and the aforementioned RBOH signaling, are depicted in the diagram below (Fig. 7.3).

7.9 Conclusion/Future Directions

Plants stresses leads to the production of ROS, responsible for oxidative damages. The protective mechanisms consist of the production of enzymatic and non-enzymatic antioxidants. Indirect antioxidants can either directly act on ROS or by interceding signaling networks. This chapter provides detailed functions of melatonin in plant tolerance to abiotic stresses, especially the crosstalk with signal molecules like NO, H_2S, and ROS. At non-damaging concentrations, ROS act as signal molecules to induce stress tolerance. The role of melatonin in activating ROS signal via RBOHs regulation was shown. However, the exact process of melatonin-mediated plant tolerance by signaling molecules is still fragmentary. More insights are expected to shed more light on how ROS (from other sources) affect the melatonin-mediated oxidative stress tolerance. As this knowledge could shift the paradigm of crop stress tolerance by providing unique route to monitor all the antioxidant machinery of plants for an optimum response.

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Reactive Nitrogen Species (RNS) and Melatonin Interaction in Plant

8

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Abstract

It is a well-known fact that plant productivity is greatly affected when multiple stresses are present together, as evidenced by the 30% reduction in total European agricultural production caused by heat waves and severe drought episodes. The important molecular subgroups predominantly created by aerobic organisms by virtue of these stresses are reactive nitrogen species (RNS). RNS can be divided into two groups according to their chemical structure: free radicals and non-radicals. A major RNS in plants, nitric oxide (NO), is created by various enzymatic and non-enzymatic mechanisms. RNS have a significant role in controlling plant metabolism, development and their response to diverse biotic and abiotic stresses. NO functions as a signaling molecule in the growth and development of plants. Melatonin is essential for boosting plant physiological activities, particularly by protecting plant tissues from a variety of environmental stressors. Melatonin could lower oxidative damage through inhibition of NO production and NO synthase activity and it may work in conjunction with NO to strengthen plant defenses. Nitric oxide (NO) and melatonin cross-talk plays a distinct role in governing redox homeostasis in cells. Melatonin regulate NO production induced by polyamines in plants. Melatonin and NO can both alter the expression of a number of transcription factors (TFs) and hormone signaling

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components, hence enhancing plants' overall anti-stress response. More research is needed to outline the precise roles of endogenous melatonin and NO as well as the effects of various stressors on their cross-talks. Finally, identifying novel melatonin and NO receptors and downstream signaling pathways may provide insights into their interactions and mechanisms of action, ultimately leading to the development new strategies for improving plant stress tolerance.

Keywords

Reactive nitrogen species (RNS) · Melatonin · Cross-talk · Interaction · Signaling · Biotic stress · Abiotic stress

8.1 Introduction

In the foreseeable future, climate change occurrences are expected to intensify the impact of environmental stressors on plant production across many regions worldwide (Piao et al. 2019; Chourasia et al. 2021). This climate change challenges the global food supply, since it is predictable that the world's population will reach 9.7 billion by 2050. It is well known that plant productivity is greatly affected when multiple stresses are present together (Zandalinas et al. 2019), as evidenced by the 30% reduction in total European agricultural production caused by heat waves and severe drought episodes (Ciais et al. 2005). Two important molecular subgroups predominantly created by aerobic organisms are reactive oxygen and reactive nitrogen species (ROS and RNS) (Corpas and Palma 2018). Nitric oxide (NO), one of the chief RNS, was initially detected in plants in the 1960s but was not assigned the same importance as ROS until the 1990s. Nitric oxide (NO) is now understood to operate as a signaling molecule in plant diseases, which has rekindled interest in studying the physiological roles and molecular pathways of RNS in plants (Khan et al. 2021). Reactive oxygen species (ROS) were formerly thought to be harmful chemicals, but subsequently, it was discovered that they were only signaling molecules (Pande et al. 2021). Reactive nitrogen species (RNS), on the other hand, were initially recognized as signaling molecules. RNS also have a significant role in controlling plant metabolism, development and their response to diverse biotic/abiotic stresses (Pande et al. 2022). The production of RNS can be triggered by various environmental stressors, including intense light, salt, high temperature or cold, drought, waterlogging, and plant pathogens (Ali et al. 2022; Jan et al. 2022; Rahim et al. 2022).

8.2 Reactive Nitrogen Species (RNS)

Reactive nitrogen species are highly reactive molecules that can be divided into two groups according to their chemical structure: free radicals and non-radicals (Kwon et al. 2021). The free radical RNS group consists of nitric oxide (NO), nitrate trioxide

(NO_3), and nitric dioxide (NO_2) while the non-radical RNS group includes nitroxyl anion (NO^-), peroxynitrite ($NOOO^-$), dinitrogen tetroxide (N_2O_4), nitrous acid (HNO_2), nitrosonium cation (NO^+), and dinitrogen trioxide (N_2O_3) (Laxa et al. 2019). The biological effects of NO, which can have both pro-oxidant and antioxidant properties, depend on its concentration and method of generation. Under environmental stress, there are several mechanisms through which NO can regulate protein function (Sami et al. 2018). A major RNS in plants, nitric oxide (NO), is created by various enzymatic and non-enzymatic mechanisms (Farnese et al. 2016). RNS are typical by-products of many metabolic processes, but their primary source is the electron transport chains (ETC) found in chloroplast and mitochondria (Considine and Foyer 2021).

In contrast to the formation of ROS, the mechanism by which NO is produced in plant cells is still poorly understood. In higher plants, there is no nitric oxide synthase (NOS), which is the primary generator of NO in animals. The production of NO by plants can be attributed to oxidative and reductive pathways. NO is produced by oxidative pathways using arginine, polyamines, and hydroxylamine, while reductive pathways use XOR (xanthine oxidoreductase) and NiNOR (nitrite NO-reductase). Plant organelles such as chloroplasts, cell walls, cell membranes, mitochondria, cytoplasm, and peroxisomes produce reactive nitrogen species (Farnese et al. 2016). Environmental stresses can seriously harm plants' molecular, biochemical, and physiological systems, which reduces crop yield and increases the risk of nitrosative stress from excessive RNS production (Corpas and Palma 2018; Corpas et al. 2023). As a result of biotic and abiotic stresses, nitric oxide (NO) plays an important role in the growth and development of plants. Multiple studies have shown how NO controls the development and growth of plants under stress (Ali et al. 2022; Rahim et al. 2022).

8.2.1 Role of RNS in Plants

Unlike ROS, which are better understood, the mechanisms by which RNS are produced in plants are under investigation (Mangal et al. 2023a, b). Nitric oxide, a small signaling molecule that contributes significantly to many physiological aspects of plant growth, is still poorly understood in plants (Astier et al. 2018). In recent years, studies have demonstrated that the mitochondrial ETC (electron transport chain) is crucial to regulating NO generation in plants when environmental stress occurs (Gupta et al. 2018). Unlike in animals, the presence of nitric oxide synthase (NOS) in higher plants has not been established, despite reports of its involvement in NO synthesis in plant extracts from various species (Alderton et al. 2001; Gupta and Igamberdiev 2015). The oxidation of L-arginine to NO and citrulline, using oxygen and NADPH, is catalyzed by the complex reaction involving FAD, tetrahydrobiopterin (BH4), FMN, Ca^{2+}, and calmodulin in plants (Knowles and Moncada 1994; Alderton et al. 2001). Contrary to *Arabidopsis thaliana*, which lacks any genes or proteins that resemble mammalian NOS enzymes, attempts to clone a higher plant nitric oxide synthase (NOS) gene based on animals NOS sequences have failed (The Arabidopsis genome initiative 2000; Del Río 2011). The only characterized NOS in plant kingdom is found in the unicellular green alga *Ostreococcus tauri* (Foresi et al. 2010).

Reactive nitrogen species (RNS) are highly reactive molecules that include free radicals and non-radicals. These compounds may cause nitrosative stress, which is analogous to oxidative stress and are synthesized by plants in response to biotic and abiotic stimuli (Tan et al. 2007; Kapoor et al. 2019). S-nitrosylation, mediated by RNS, is a crucial post-translational modification that controls cellular signaling and metabolism. It forms an *S*-nitrosothiol (SNO) bond by transferring a nitric oxide (NO) group to a cysteine residue on a protein. This alteration may change enzymatic activity or protein–protein interactions, among other aspects of protein function. In response to abiotic stress, RNS and S-nitrosylation play a significant role in plants. In this regard, *S*-nitrosoglutathione (GSNO) synthesis and glutathione activation are essential (Begara-Morales et al. 2018). Additionally, *S*-nitrosothioles like *S*-nitrosoglutathione (GSNO) may act as NO donors and contribute significantly to the enhanced NO levels in plants (Leterrier et al. 2011). Begara-Morales et al. (2018) outlined several techniques employed for detecting levels of nitric oxide (NO) and *S*-nitrosothiol (SNO) in plants, as well as the processes involved in the turnover of *S*-nitrosoglutathione (GSNO). Signaling specificity of NO is significantly influenced by protein denitrosylation, and the elimination of S-nitrosylation through GSNO reductase and thioredoxin h5 (Trxh5) is as critical as its generation (Umbreen et al. 2018). Researchers have also investigated the role of RNS in fruit ripening, specifically in pepper and tomato, to enhance fruit yield and quality using a translational approach (Corpas et al. 2018b). It is evident that NO regulates various cycles by activating quality records or signaling secondary messengers (Besson-Bard et al. 2008; Gaupels et al. 2011). Two modes of synthesis have been proposed for the production of RNS in plants. The oxidative pathway, in which nitric oxide synthases (NOSs) enzyme is involved, and the reductive pathway, in which nitrites are reduced to NO by nitrate reductase (NR) enzyme (Zhao et al. 2007; Kataria et al. 2020). Arginanine, polyamines, and hydroxylamine are the oxidative pathway's substrates for NO production (Del Río 2015). Xanthine oxidoreductase (XOR) activity in peroxisomes and NO-reductase (NiNOR), which is tethered to the membrane, are both part of the reductive process (Farnese et al. 2016). The cytosolic enzyme nitrate reductase (NR) is also essential to plants' ability to produce nitric oxide. NR contributes significantly to generating NO during bacterial defense, in the presence of other pathogens, during drought stress, for cold adaptation, stomatal opening control, in lowering symptoms of iron (Fe) deficiency, and during root development (Farnese et al. 2016). According to earlier studies, nitrate reductase (NR) prefers to convert nitrate into nitrite in normal situations. Nitric oxide (NO) generation can be increased by NR in some circumstances, such as anaerobic environments or higher nitrate contents (Mur et al. 2013). Nitrosative stress controls a number of pathways, including the Ca^{2+}-dependent pathway in the roots of *Hylotelephium erythrostictum* (Chen et al. 2019), the SOS pathway in rapeseed (Zhao et al. 2018), the G-protein and MAPK-dependent pathway in Arabidopsis (Li et al. 2009), and maize (Bai et al. 2011). These pathways all help plants withstand the negative effects of high salinity.

Plants can generate nitric oxide (NO) through both enzymatic and non-enzymatic systems (Hancock 2012; Mur et al. 2013; Del Río et al. 2014), with L-arginine-dependent NOS action being reported in extracts from various plant species (Jasid et al. 2006; Corpas et al. 2009; Del Río 2011). The subcellular locations where NO is produced in plant systems are not well known (Barroso et al. 1999; Del Río et al. 2006; Del Río 2011), but studies have shown that NO can be generated in peroxisomes, chloroplasts, and mitochondria (Gupta and Kaiser 2010). Nitric oxide is a crucial signaling molecule in plant growth and development, playing a role in numerous physiological processes such as seed germination, cell wall lignification, root organogenesis, pollen tube growth, legume-Rhizobium symbiosis, flowering, fruit ripening, senescence, and response to biotic and abiotic stress (Mata and Lamattina 2001; Wendehenne and Hancock 2011; Khan et al. 2014; Yu et al. 2014). Farvardin et al. (2020) reported that RNS and its derivatives are produced in various cellular locations, including the apoplastic regions, plasma membrane, cytoplasm, chloroplasts, mitochondria (Gupta et al. 2018), and peroxisomes (Corpas et al. 2020) under salinity stress. Multiple studies have been conducted on different plant species, such as maize (Kaya and Ashraf 2021), citrus (Tanou et al. 2012), wheat (Sehar et al. 2019), cucumber (Campos et al. 2019), tomato (Manai et al. 2014), and halophytes (Chen et al. 2013), have demonstrated the beneficial effects of RNS in response to salinity stress.

8.3 Melatonin

Melatonin (*N*-acetyl-5-methoxy tryptamine) is a small molecule with an indole ring found in plants and animals. Initially, this compound was discovered in the bovine pineal gland, which affects various physiological processes, such as immunity and circadian rhythms in animals (Carrillo-Vico et al. 2013; Tiwari et al. 2021a). Although melatonin was not initially identified in higher plants, current studies suggest it is crucial for controlling growth and development and protecting plants from biotic/abiotic stresses (Zhu et al. 2019; Tiwari et al. 2021b). New research avenues have been made possible by melatonin's effects on endosperm and epidermal cells of bulbous plants and onions (Banerjee and Margulis 1973). ROS, RNS, and other harmful oxidative molecules are primarily controlled by melatonin's antioxidant activity in plant cells (Hardeland 2016). Nitric oxide (NO) and melatonin interaction play a distinct role in controlling redox homeostasis in cells (Berchner-Pfannschmidt et al. 2008; Lal et al. 2021a, b). There has been considerable research on the interaction between NO and melatonin in animal systems, and more recent research has shed light on this relationship in plant systems (Kaur and Bhatla 2016; Arora and Bhatla 2017; Klein et al. 2018; Mukherjee 2019) Melatonin could lower oxidative damage through inhibition of NO production and NO synthase activity (Aydogan et al. 2006), and it may work in conjunction with NO to strengthen plant defenses against a variety of stresses (Rodriguez et al. 2004; Tiwari et al. 2020a). The production of lateral roots, root hairs, and adventitious roots, among other auxin-induced physiological processes, are all known to be significantly influenced by the gaseous signaling molecule NO (Arnao and Hernández-Ruiz 2017). The NO-scavenging abilities of melatonin have also been observed, and the ratio of AFMK to c3HOM serves as a proxy for the severity of oxidative damage (Tan et al. 2007). Additionally, melatonin is essential for boosting plant physiological activities, particularly by protecting plant tissues from a variety of environmental stressors (Tiwari et al. 2020b). Several research conducted in this area have shown above aspect (Meng et al. 2014; Erland et al. 2015; Cui et al. 2017).

Melatonin and NO interact intricately in plants, consisting of distinct and multiple signaling pathways. Intriguing findings from recent studies that addressed this complexity have helped us better understand these relationships (Zhu et al. 2019; Lal et al. 2021a, b). Numerous crops, including bananas, apples, tomatoes, rice, cucumbers, and onions contain the hormone melatonin, which plants produce. It is present in various plant components, including flowers, fruits, roots, leaves, stems, seeds, and bulbs (Nawaz et al. 2016; Rahman et al. 2023). The concentration of this compound depends on the tissue types, species, cultivars, physiological processes of the plant (Erland et al. 2015). This chapter thoroughly analyzes RNS functions in plants and how they relate to melatonin. The cross-talks between melatonin and nitric oxide (NO) in growth, development, and reactions to environmental stresses in plants are outlined, and the signaling mechanisms underlying these interactions are discussed.

8.4 Melatonin Interaction with RNS (Melatonin-RNS)

Plants contain melatonin, a molecule having molecular resemblances to indole-3-acetic acid (IAA). Melatonin was found in higher plants by the Dubbels and Hattori groups in 1995 (Dubbels et al. 1995; Hattori et al. 1995). The biosynthesis and the degradation mechanisms comprise the two steps of plant melatonin metabolism. Three distinct pathways can result in the synthesis of melatonin. During the conversion of tryptophan into serotonin, two enzymes are involved, i.e., tryptophan decarboxylase (TDC) and tryptamine 5-hydroxylase (T5H) which belong to pathway I. It is then converted into melatonin by the enzymes serotonin *N*-acetyltransferase (SNAT) and hydroxyindole *O*-methyltransferase (HIOMT) or *N*-acetyl-serotonin methyltransferase [ASMT]. The identical pathway as pathway I is followed by pathway II, but in the reverse direction. Tryptophan converts to tryptamine by TDC, and tryptamine is subsequently changed into *N*-acetyl-serotonin by T5H and SNAT in pathway III. *N*-acetyl-serotonin is finally converted into melatonin by HIOMT. Plants produce melatonin primarily in chloroplasts and mitochondria (Tan and Reiter 2019). M2H (Melatonin 2-hydroxylase) is mainly responsible for facilitating melatonin breakdown, which yields 2-hydroxymelatoninatonin as its primary metabolite (Byeon et al. 2015). Melatonin content in plants is regulated by its biosynthesis and degradation. By regulating the expression of downstream genes, melatonin, serving as a crucial modulator, contributes significantly to a plant's capacity to endure abiotic stress (Wang et al. 2018). Although environmental stress can raise melatonin levels in plants, it is unclear how different growing conditions affect melatonin content. In *Glycyrrhiza uralensis*, the seed, root, stem, and leaf tissues exhibit the highest melatonin concentration. Red light was the most effective light wavelength for increasing melatonin content, whereas UV-B radiation with high intensity and brief duration enhanced melatonin levels in the roots of *G. uralensis* (Afreen et al. 2006). Melatonin has a wide variety of functions in plants, including acting as an antioxidant or hormone and protecting them from harsh weather conditions and environmental pollutants by scavenging numerous reactive oxygen species such OH, H_2O_2, ONOO, NO, HOCl, and O_2 (Tan et al. 2000). As plants evolved, the role of melatonin changed from being merely an antioxidant to becoming a hormonal signaling molecule (Tan et al. 2010). Nitric oxide (NO) is produced and removed in plants by oxidative and reductive mechanisms, respectively. During stress signaling, melatonin can react with NO through its active forms, such as c3HOM, AFMK, and AFK. It can also stimulate NO creation or scavenge excess NO (Lee and Back 2019). Melatonin has shown a higher capacity to scavenge NO than its precursors (Noda et al. 1999). *N*-Nitrosomelatoninatonin (NOMelatonina), which can function as an influential NO donor, is created when NO interacts with melatonin in the presence of oxygen (Berchner-Pfannschmidt et al. 2008; Kopczak et al. 2007). According to Arnao and Hernández-Ruiz (2017), nitric oxide (NO) plays a significant role in the auxin-like and immunological responses that melatonin induces in plants.

Additionally, it controls the growth of adventitious roots, root hair, and lateral roots. Although high NO concentrations can affect plants through oxidation, the AFMK to c3HOM ratio can measure the degree of oxidative injury (Tan et al. 2007). NO is an essential signaling molecule for plant growth, development, and survival when present in sufficient amounts. According to research, the management of day–night cycles and the production of melatonin in photoreceptors have also been linked to melatonin (Wellard and Morgan 1996). Additionally, it has been shown that NO can change the structure of glycolytic enzymes and that melatonin can reverse this effect (Strumillo et al. 2018; Thakur et al. 2023). Melatonin has been found to promote adventitious root development in tomato seedlings by upregulating genes involved in NO production (Wen et al. 2016). Additionally, it has been discovered that melatonin functions as an antioxidant that scavenges free nitrogen species during the ripening of tomato fruits (Corpas et al. 2018b). Plants may communicate across long distances using NOMelatonina, a melatonin derivative generated through nitrosation (Mukherjee 2019; Mukherjee and Bozhkov 2019). Melatonin has been reported to modify NO synthesis, which delays postharvest senescence in pears and controls ethylene production (Liu et al. 2019). Furthermore, arylalkylamine-*N*-acetyltransferase (AA-ANT) activity could be suppressed by NO (Wellard and Morgan 2004), which raises cGMP levels, in order to assist in the photoperiodic control of melatonin production through cGMP (Zipfel et al. 2002).

Several studies have shown that melatonin treatment increases disease resistance and plant tolerance to various stressful events (Bairwa et al. 2023). Melatonin and NO have complementary physiological roles in plant systems and interact with one another (Zhu et al. 2019; Mukherjee 2019). It has been demonstrated that NO plays a role in melatonin-mediated plant responses to stress, with melatonin controlling NO levels to the advantage of plants under stress. NO, and melatonin (MET) collaborate to promote plant development and modulate the tolerance to abiotic stress by controlling the antioxidant production and release in the system (He and He 2020). By increasing the activity of NOS-like proteins, melatonin can enhance NO synthesis, scavenge excessive NO, and promote NO accumulation (Aghdam et al. 2019; Liu et al. 2019). Numerous signaling pathways and different activities are part of the complex interaction between NO and melatonin (He and He 2020). Treatments with $ZnSO_4$, NaCl, and H_2O_2 result in a time-dependent increase in the melatonin concentration in barley roots, as shown by experiments using liquid chromatography-mass spectrometry (LC-MS) and fluorescent LC detection (Arnao and Hernández-Ruiz 2009). Exogenous melatonin can upregulate the expression of genes involved in cold signaling, such as cold-responsive genes (COR15a) and C-repeat-binding factors (CBFs), which reduces the effects of primary abiotic stressors in Arabidopsis (Bajwa et al. 2014). Additionally, Aghdam et al. (2019) discovered that melatonin-triggered NO accumulation confers chilling tolerance in tomato fruits. Also, it has been shown that 2-hydroxymelatonin increases tobacco and tomato plant resistance to combined effect of cold and drought stress (Lee and Back 2019). Plants are protected by melatonin and NO from various abiotic stressors, such as salt, aluminum, and drought. In sunflower seedlings under salt (NaCl) stress, melatonin and NO regulate glutathione content and glutathione reductase (GR) activity to prevent the harmful effects of RNS and ROS (Kaur and Bhatla 2016; Arora and Bhatla 2017). Melatonin affects nitro-oxidative redox homeostasis to reduce oxidative damage during drought stress in Lucerne (Antoniou et al. 2017). By restoring equilibrium to redox homeostasis and the Na^+/K^+ ratios through NO-mediated antioxidant enzyme activity, melatonin also improves the salt tolerance of Brassica seedlings (Zhao et al. 2018). In addition, the cross-talk between NO and H_2S contributes to the pepper's melatonin-induced resistance to salt stress (Kaya et al. 2020). It is interesting to note that melatonin restricts the production of NO in Arabidopsis to reduce the suppression of root development caused by aluminum (Zhang et al. 2019). By raising endogenous NO levels, which are then decreased by the NO scavenger cPTIO, melatonin treatments have been found to reduce Cd stress in wheat plants (Lee et al. 2017). Additionally, studies point to a function for NO in the control of COMT and TDC in rice. Melatonin-induced endogenous NO generation in wheat seedlings lowers oxidative stress and improves cadmium (Cd) tolerance (Kaya et al. 2019, 2020). Furthermore, NO participates in melatonin-induced antioxidant responses in *Catharanthus roseus* roots during Cd toxicity stress (Nabaei and Amooaghaie 2019), which aid in boosting antioxidant enzyme activity and Cd translocation (Nabaei and Amooaghaie 2020). Melatonin helps Arabidopsis overcome an iron deficit by increasing the accumulation of polyamines and the concentration of NO to upregulate the expression of genes for iron (Fe) acquisition (Zhou et al. 2016). Also, evidence points to an integration of NO and H_2S with melatonin-induced tolerance of iron deficiency in pepper plants (Kaya et al. 2020). Okant and Kaya (2019) have discovered that the increased activity of specific antioxidant enzymes is responsible for the tolerance of maize to lead (Pb) toxicity induced by melatonin-mediated NO. The study by Liu et al. (2015)

has also reported that melatonin treatment elevates NO levels, which enhances the antioxidant system, reduces Na^+ buildup, and improves tomato tolerance to alkaline stress. These findings are represented in Table 8.1. Melatonin has been found to improve the tolerance of *Haematococcus pluvialis* to intense light and nitrogen deficiency by triggering the cAMP signaling pathway and NO-mediated MAPK signaling cascade, leading to increased astaxanthin synthesis (Ding et al. 2018). Melatonin has also been demonstrated to improve Arabidopsis's innate defenses against *Pseudomonas syringe* pv. tomato (Pst) DC3000 by raising levels of SA and ethylene, reducing pathogen susceptibility (Lee et al. 2014). According to Lee and Back (2017), NO- and H_2O_2-dependent pathway results in the disease resistance against Pst DC3000 infection offered by melatonin application. Additionally, it has been found that melatonin therapy boosts tomato resistance to TMV by accumulating NO and SA (Zhao et al. 2019). These findings imply that melatonin regulates plant stress response and disease resistance by activating a variety of signaling pathways as represented in Table 8.2. However, Kaya et al. (2019) found that the use of NO inhibitors can negate the beneficial effects of melatonin, increasing the generation of ROS and oxidative stress.

It is fascinating to see the range of stress factors that melatonin can alleviate in plants and how it interacts with NO and other signaling pathways to confer stress tolerance (Mangal et al. 2023a, b; Rather et al. 2022). The involvement of NO in many of these processes highlights its essential role in plant stress responses and its cross-talk with melatonin (Watpade et al. 2023). Melatonin interacts with RNS in plants complexly, modulating their production and activity through various mechanisms. The ability of melatonin to interact with RNS is critical under conditions of environmental stress, where RNS plays a crucial role in plant defense responses (Kumar et al. 2023a, b). It will be interesting to see how further research deepens our understanding of these intricate interactions and how they might be used in agriculture and environmental management to create novel strategies for increasing plant resiliency to environmental stresses.

8.5 Melatonin-Mediated Regulation of RNS Synthesis and Signaling

Melatonin is a versatile molecule that is critical in regulating diverse physiological processes in plants, including modulating reactive nitrogen species (RNS) signaling (Altaf et al. 2023). Highly reactive RNS molecules are generated in response to a variety of environmental stressors. Recent years have witnessed the emergence of an emerging area of research as a result of the discovery that plant cells could generate free radical nitric oxide (NO) (Kolbert et al. 2019). The enzymatic source of nitric oxide (NO) in higher plants remains unidentified in contrast to mammals, where nitric oxide synthases (NOS) are in charge of producing NO from the amino acid L-arginine. Melatonin's role in regulating RNS signaling is crucial for plant overall development and stress responses. Nitric oxide (NO) synthesis in higher plants can be broadly attributed to two pathways (Lal et al. 2023). The first pathway uses a

Table 8.1 The interaction between melatonin and NO in abiotic stress responses of plants

S. no.	Stress	Crop	Dose and duration	Melatonin concentration (μM)	Function/effect	References
1.	Cold	*Arabidopsis thaliana*	4 °C for 72 and 120 h on leaf	10 and 30	The genes CBF, COR15a, CAMTA1, and ZAT10/12 are being upregulated	Bajwa et al. (2014)
		Solanum lycopersicum	4 °C for 28 days on fruit	–	The up-regulation of ZAT2/6/12 genes can enhance chilling tolerance in fruits by promoting the production of polyamines and proline	Aghdam et al. (2019)
			4 °C for 48 h on plant	100	Various factors including gene expression, enzyme activity, and substrate availability regulate polyamine synthesis	Ding et al. (2017)
			4 °C for 24 h on plant	–	Polyamines can mediate the synthesis of nitric oxide (NO)	Diao et al. (2017)
			4 °C for 28 days on fruits	100	The activity of the arginine pathway can lead to the production of polyamines (PAs) and the accumulation of nitric oxide (NO)	Aghdam et al. (2020)
		Cucumis sativa	5 °C for 72 h	100	The increase in activity of NR (nitrate reductase) and content of NO can upregulate mRNA expression of NR-related genes	Feng et al. (2021)
		Nicotiana benthamiana	4 °C for 30 days on leaf	10	Activating melatonin 2-hydroxylase can lead to the conversion of melatonin to 2-hydroxymelatonin	Lee and Back (2019)
2.	Drought	*Solanum lycopersicum*	30 days on leaf	10	Activating melatonin 2-hydroxylase can lead to the conversion of melatonin to 2-hydroxymelatonin	Lee and Back (2019)
		Arabidopsis thaliana	Leaf	–	Nitric oxide synthase (NOS) activity can contribute to salt stress tolerance in plants	Shi et al. (2015b)

		Glycine max	10 days on plant	100	Increase in the level of NO within plants	Imran et al. (2021)
		Medicago sativa	7 days stress on leaf	10	Changes in proline metabolism can improve the response to drought stress, and proline metabolism can be modulated to enhance this effect	Antoniou et al. (2017)
3.	Salinity	*Helianthus annuus*	120 mM on cotyledon	15	GSH (glutathione) content and the activity of GR (glutathione reductase) can be modulated	Kaur and Bhatla (2016)
		Zea mays	150 mM NaCl	–	Control of superoxide dismutase (SOD) activity can enhance salinity stress tolerance	Klein et al. (2018)
		Arabidopsis thaliana	Leaf	–	NOS (nitric oxide synthase) activity can enhance salinity stress tolerance	Shi et al. (2015b)
		Brassica napus	250 mM NaCl for 2 days on seedlings	1	Re-establishing redox and ion homeostasis, modulating genes related to antioxidant defense, and regulating the expression of NHX1 and SOS2 can enhance salinity stress tolerance. During this process, a temporal surge in the accumulation of endogenous NO and melatonin can also occur in Brassica seedlings	Zhao et al. (2018)
		Helianthus annuus	120 mM on cotyledon	15	The expression of different types of SODs can be modulated to improve salt stress response	Arora and Bhatla (2017)
		Zea mays	100 mM on root	–	NO induces nutritional and physiological changes in plants in salinity stress	Kaya et al. (2018)
		Capsicum annuum	100 mM NaCl on leaf	100	There is an integration between NO and H_2S signaling pathways in plants	Kaya et al. (2020)
		Triticum aestivum (L.)	12.0 dS m^{-1} on plants	70	Melatonin and salicylic acid can enhance plant salinity tolerance by inducing changes in nitrogen metabolism. Additionally, the application of melatonin and SA can increase	Talaat (2021)

(continued)

Table 8.1 (continued)

S. no.	Stress	Crop	Dose and duration	Melatonin concentration (μM)	Function/effect	References
					the content of Spd (spermidine), Spm (spermine), and Pas (polyamines)	
4.	High temperature	*Solanum lycopersicum*	42 °C, 24 h	100	Melatonin treatment can lead to an increase in the endogenous content of NO	Jahan et al. (2019)
5.	Heavy metal	*Arabidopsis thaliana*	200 μM aluminum on root	10	The expression of *AtSNAT* can be downregulated	Zhang et al. (2019)
		Oryza sativa	0.5 mmol/L cadmium, on seedling	~600 ng/g	TDC and COMT can be regulated	Lee et al. (2017)
		Triticum aestivum	Cadmium; leaf	50 and 100	The activity of superoxide dismutase, catalase, and peroxidase can be increased. Enhanced growth attributes and reduced oxidative stress can be achieved by decreasing endogenous NO levels	Kaya et al. (2019)
		Catharanthus roseus	200 μM cadmium; root	100	Promoting antioxidant response	Nabaei and Amooaghaie (2019)
		Catharanthus roseus	200 mg kg^{-1} cadmium; leaf	100	Enhance the antioxidant response in plants	Nabaei and Amooaghaie (2020)
		Arabidopsis	Iron deficiency; root	5	Polyamines can induce NO production	Zhou et al. (2016)
		Capsicum annuum	Iron deficiency (0.1 μM); leaf	100	NO and H_2S signaling pathways can integrate and interact with each other in plants	Kaya et al. (2020)
		Zea mays	0.1-mM $PbCl_2$ (Lead); leaf	50–100	Reducing H_2O_2 (hydrogen peroxide) and MDA (malondialdehyde) can improve the tolerance of plants to lead toxicity	Okant and Kaya (2019)

		Solanum lycopersicum	75 mM $NaHCO_3$ for 10 days (sodic-alkaline); leaf	0.5	Activation of the antioxidative system and reduction of Na^+ accumulation	Liu et al. (2015)
6.	High light and N starvation	*Haematococcus pluvialis*	Cell	10	The cyclic adenosine monophosphate and mitogen-activated protein kinase signaling pathways can be activated in plants	Ding et al. (2018)
7.	Fruit ripening	*Capsicum annum*	Fruit	0.1–15	Melatonin and NO can delay fruit ripening	Mukherjee (2019)
8.	Chemical pollutants	*Tabacum* spp.	Foliar spray	100	The expression of SAMS1, SAMS2, and SAMS3 genes can lead to enhanced levels of SAMS1, SAMS2, and SAMS3 proteins in plants	Wang et al. (2022)

Table 8.2 The interaction between melatonin and NO in biotic stress responses of plants

S. no.	Biotic agent	Crop	Dose and duration	Melatonin conc. (μM)	Effects	References
1.	**Bacteria**					
	Pseudomonas syringae pv. tomato DC3000	*Arabidopsis thaliana*	Added to nutrient solution	20	Innate immunity response to bacteria can be improved	Shi et al. (2015a)
			Leaf treatment	1	The mitogen associated proteinase kinase signaling pathway can be activated in response to bacteria, leading to an improved innate immune response. Activation of MAPKKK3 and OXI1	Lee and Back (2017)
			Leaf	10	The levels of salicylic acid and ethylene can increase in plants	Lee et al. (2014, 2015)
			Added to nutrient solution	Watering with 20–100 μM melatonin	The induction of NO (nitric oxide), pathogenesis-related genes, can occur in plants	Zhao et al. (2007), Shi et al. (2015a, b), Qian et al. (2015)
	Many pathogens	*Arabidopsis thaliana, Nicotiana tabacum*	Leaf	1	The MKK4/5/7/9-MPK3/6 cascade can be activated in plants under certain conditions such as stress or pathogen attack. This cascade refers to a signaling pathway where mitogen-activated protein kinases (MPKs) such as MPK3 and MPK6 are activated by MAPK kinases (MKKs) such as MKK4, MKK5, MKK7, and MKK9, leading to downstream cellular responses	Lee and Back (2016)
	Pseudomonas syringae DC3000	*Nicotiana tabacum*	Leaf	10	The levels of salicylic acid and ethylene can increase in plants	Lee et al. (2014)

	X. oryzae pv. oryzicola	*Oryza sativa*	Leaf	Treating with 20–100 μg mL^{-1} melatonin (86 μM)	The activation of NO can lead to improved resistance in plants	Chen et al. (2020)
2.	**Virus**					
	Tobacco Mosaic Virus (TMV)	*Nicotiana glutinosa* and *S. lycopersicum*	Irrigated to root	100, 200	Improved plant resistance to infection through the action of SA and NO	Zhao et al. (2019)
	Rice black-streaked dwarf virus	*Oryza sativa*	Pre-treatment of plants	10	The signaling pathway involving nitric oxide results in an increase in melatonin content, which enhances the defense response against viral infections	Lu et al. (2020)

nitrate and nitrite-based reductive mechanism catalyzed by nitrate reductase (NR). The second pathway involves an oxidative mechanism resulting from nitric oxide synthase (NOS)-like activity induced by L-arginine (Corpas et al. 2022; Astier et al. 2018). NO synthesis depends heavily on polyamine metabolism, and polyamines control NO levels via the NR and arginine-linked NOS pathways (Talaat 2021). Melatonin has been proposed to regulate NO production induced by polyamines in plants (Aghdam et al. 2019; Zhou et al. 2016). Numerous related molecules, including nitrogen dioxide (NO_2), *S*-nitrosoglutathione (GSNO), and peroxynitrite ($ONOO^-$) are produced during the metabolism of NO (Corpas 2017). When both NO and O_2 radicals coexist in a plant subcellular location, $ONOO^-$, a highly reactive molecule, is created (Ferrer-Sueta et al. 2018). Numerous studies have demonstrated the regulatory function of melatonin in plants' NO production. *S*-nitrosoglutathione (GSNO) is produced when NO binds to the thiol group of reduced glutathione. Post-translational modifications (PTMs) are known to control protein activities in plants by reactive nitrogen species (RNS). Tyrosine nitration is an irreversible event that typically inhibits the targeted proteins (Radi 2013; Mata-Pérez et al. 2016), in contrast to S-nitrosation, which is a reversible process that can both increase and decrease plant enzyme activity (Corpas et al. 2008; Gupta et al. 2020).

The interaction between melatonin and its PMTR1 receptor, which upregulates the synthesis of critical enzymes like nitric oxide synthase (NOS-like) and nitrate reductase, causes an increase in nitric oxide (NO) levels. By directly scavenging reactive nitrogen species (RNS) through enzymes involved in production and breakdown, melatonin controls the internal levels of RNS. Additionally, melatonin interacts with $O_2^{\bullet-}$ or NO-biosynthetic enzymes to create peroxynitrite ($ONOO^-$), altering RNS levels. Studies have demonstrated an interaction between melatonin and $ONOO^-$ that may provide cellular protection against protein nitration in stressful environments (Corpas et al. 2022). Due to its strong coupling activity, the generation of $ONOO^-$, accompanied by an increase in nitric oxide ($^\bullet NO$) and $O_2^\bullet$, may have adverse effects. Therefore, the interaction between $ONOO^-$ and melatonin offers an extra defense against protein nitration, especially under adverse conditions, requiring further research. Nitric oxide (NO) has been linked to melatonin responses, including auxin-like and plant immunological responses, which are important signals that become more prominent during biotic/abiotic stress (Astier et al. 2016; Yusuf et al. 2013). Similar to how hydrogen peroxide (H_2O_2) is extensively researched, NO is also examined for its role in signaling in plant cells (Kohli et al. 2019; Corpas et al. 2018a; Gupta et al. 2022). In the melatonin signaling system, the NO signaling pathway is regarded as a downstream signal (He and He 2020), and polyamines have been found to interact with RNS in response to abiotic stressors (Alcázar et al. 2010). NO has powerful antioxidant and signaling properties that help plants tolerate salinity better. In sunflower and rapeseed seedlings, melatonin operates with NO-dependent S-nitrosylation pathways to enhance plant tolerance to NaCl stress. NO is generated by two enzymatic routes, the nitrate/nitrite-dependent pathway and the L-Arg-dependent mechanism. Through post-translational modifications, NO can regulate the reactive oxygen species (ROS) network, alleviating stress and cellular damage (León et al. 2016). By upregulating melatonin biosynthesis genes, endogenous melatonin levels rise in response to abiotic and biotic stress (Wen et al. 2016; Wei et al. 2018). Melatonin increases NO levels and acts as an NO and ROS scavenger, while NO acts downstream of melatonin signaling to regulate stomatal closure (Li et al. 2017). Nitric oxide (NO) is a second messenger in melatonin signaling in Arabidopsis nia1/2 and noa1 mutants, based on experimental findings. Melatonin and NO can both alter the expression of a number of transcription factors and hormone signaling components, hence enhancing plants' overall anti-stress response.(Verma et al. 2016; Arnao and Hernández-Ruiz 2018). Recent research suggests that NO and melatonin response may be involved in redox signaling and long-distance communication (Mukherjee 2019). The ability of melatonin to scavenge reactive nitrogen species (RNS) involves two mechanisms: hydrogen transfer and single electron transfer (Reiter et al. 1993). Plant tolerance to various stressors may be enhanced by melatonin and NO (Galano and Reiter 2018).

8.6 Cross-talk Between Melatonin and RNS in Abiotic Stress

Abiotic stress disrupts the balance of reactive nitrogen species (RNS) in plant cells, which causes an increase in internal RNS levels and induces nitrosative stress. This nitrosative stress triggers the expression of melatonin biosynthetic genes, i.e., T5H, COMT, TDC, SNAT, and ASMT, leading to endogenous melatonin biosynthesis. In Capsicum annum, a solanaceous vegetable, melatonin (MEL) was found to improve tolerance against iron deficiency and salt stress by facilitating signal cross-talk with nitric oxide (NO) and hydrogen sulfide (H_2S). Application of exogenous melatonin significantly upregulated production of NO and H_2S in stressed plants compared to control plants. Interestingly, the beneficial effects of melatonin on plant growth were reversed when a scavenger of NO was added, indicating that endogenous NO is necessary for the stimulating effect of melatonin on plants under adverse environmental conditions. Liu et al. (2015) proposed that NO functions as a downstream signal in melatonin-induced sodic-alkaline stress mitigation. Exogenous melatonin supplementation was found to have a greater effect on NO accumulation in plants, while exogenous NO application had little or no effect on endogenous melatonin's increased level under stress. A 100 μM MEL exogenous spray dramatically increased endogenous NO buildup and NOS gene expression in tomato fruits exposed to chilling conditions, resulting in increased membrane activity (Aghdam et al. 2019). Melatonin-NO cross-talk controls adventitious root development in tomato, which is important for abiotic stress tolerance (Wen et al. 2016). Melatonin also plays a role in response to drought stress and recovery in maize plants and in defense of plants under Fe-deficient conditions through polyamine-induced NO production (Fleta-Soriano et al. 2017). Melatonin can alleviate salt toxicity in wheat and heat-induced adversities in tomato seedlings by promoting polyamine modulation and NO generation (Zhou et al. 2016). Melatonin has been shown to repress salt toxicity in wheat and alleviate heat-induced adversities in tomato seedlings by promoting polyamine modulation and NO generation (Jahan et al.

2019). Additionally, melatonin dip treatment enhances freezing tolerance in tomato fruits by triggering the arginine pathway (Aghdam et al. 2019). Melatonin is a potent antioxidant that neutralizes hydroxyl radical and scavenges superoxide and NO radicals more effectively than other antioxidants. It also stimulates glutathione synthesis and counteracts oxidative stress induced by various agents. Melatonin interacts with NO and plays important role in abiotic stress responses in plants, as represented in Table 8.1. Furthermore, melatonin is involved in active nitrogen metabolism by increasing the activities of nitrogen metabolism-related enzymes, such as glutamine synthetase, glutamate synthase, nitrite reductase, and nitrate reductase (Tiwari et al. 2022).

8.7 Cross-talk Between Melatonin and RNS in Biotic Stress

In response to pathogen infection, a model for the interaction of melatonin, salicylic acid (SA), nitric oxide (NO), and reactive oxygen species (ROS) has been put forth. Through ROS, pathogens attack elevated levels of NO, SA, and melatonin (Lee et al. 2016, 2017). In cherry tomato fruits, melatonin has been found to induce disease resistance response against Botrytis cineraria by reducing lesion diameter and disease severity while enhancing SA accumulation and the expression of defense genes (Li et al. 2022). An optimal concentration of 0.1 mmol L^{-1} of melatonin reduced lesion diameter and disease severity on artificially inoculated fruits while enhancing SA accumulation and the expression of defense genes, such as SlGLU, SlTGA5, SlNPR1, SlPR1, SlPR2, and SlWRKY70 (Li et al. 2022). During the 12- to 36-h period of storage, melatonin-treated fruits had considerably higher NADPH oxidase (NOX) activity, and within 12–24 h of exogenous melatonin application, SlNOX expression was similarly raised. Melatonin treatment in tomato reduces NO release or scavenges NO, leading to the denitrosylation of respiratory burst oxidase homolog (RBOH) and the promotion of RBOH-dependent hydrogen peroxide (H_2O_2) production, indicating that RBOH activity and H_2O_2 signaling are integral components of melatonin-driven stress regulation in *Solanum lycopersicum* (Gong et al. 2017). When Arabidopsis is attacked by pathogens, melatonin production can be triggered, leading to the activation of MAPK kinase like oxidative signal induced kinase 1, followed by MAPK kinase 4/5/7/9 and MAPK3/6 cascades. This process results in upregulating several defense genes, including PR1, ICS1, GST1, and APX1 (Lee et al. 2015; Lee and Back 2016, 2017). Studies using the Arabidopsis/*Pseudomonas syringae* DC3000 (avrRpt2) model have also shown that melatonin-induced defense signaling pathways are triggered by MAPKKK3 and OXI1 kinases (Lee et al. 2016, 2017). Melatonin and NO can also promote JA production, raise sugar and glycerol levels, and activate genes that are associated with pathogens. Additionally, melatonin postpones leaf senescence, slows changes in leaf ultrastructure, increases photosynthesis, and modifies stress genes, all of which aid in protecting plants from stress environments (Zhang et al. 2015). Table 8.2 illustrates how the interaction between melatonin and NO regulates biotic stress responses in plants. Melatonin's ability to regulate RNS signaling in plants is crucial for their growth, development, and stress responses. Additionally, melatonin has been shown to enhance the innate immunity of Arabidopsis against *Pseudomonas syringe* pv. tomato (Pst) DC3000 through the accumulation of glycerol and sugars, involving NO and SA, and by increasing the levels of SA and ethylene, thus reducing pathogen susceptibility (Lee et al. 2014). According to Lee and Back (2017), the disease resistance against Pst DC3000 infection provided by melatonin application is caused by the activation of MAPK kinase kinase 3 (MAPKK3) and oxidative signal-inducible 1 (OXI1) through NO- and H_2O_2-dependent pathways. Furthermore, it has been discovered that melatonin therapy increases tomato resistance to TMV by causing the buildup of NO and SA (Zhao et al. 2019). The molecular pathways regulating RNS signaling by melatonin are complex and involve the modulation of various proteins and enzymes.

Further research is needed to understand the complex molecular mechanisms underlying the regulation of RNS signaling by melatonin in plants and develop new strategies for improving plant stress tolerance. However, the existing evidence suggests that the interaction between melatonin and RNS plays a crucial role in various physiological processes, including overall plants' development and stress responses. Melatonin regulates NOS activity and NO biosynthesis and interacts with ROS, SA, and MAPK signaling pathways to modulate plant responses to various stresses. Therefore, using melatonin as a plant growth regulator and stress protectant has significant potential in agricultural and horticultural industries.

8.8 Conclusion and Future Prospects

The cross-talk between reactive nitrogen species and melatonin is a promising area of research for understanding plant responses to both biotic and abiotic stress. While both RNS and melatonin have been studied individually, their interaction and mechanisms of action are not yet fully understood. Recent studies have shown that melatonin can directly scavenge RNS, enhance antioxidant activities, regulate plant growth regulators, and increase osmotic metabolites, thus increasing plant stress tolerance. Additionally, melatonin has been shown to be involved in the nitric oxide signaling pathway, which is crucial for plant responses to environmental stress.

However, there is still much to learn about the specific QTL and genes involved in the regulation of biosynthesis of MET and NO. Also, core pathways regulated by melatonin and NO, as well as the different responses of plants to various types of stress have not yet been extensively explored. Additionally, identifying S-nitrosation target proteins and a better understanding of the NO signaling pathway will be important for elucidating the precise mechanisms underlying the roles of melatonin and NO in regulating ROS and RNS under abiotic stress conditions.

Further investigations into the interactions between RNS and melatonin are required, particularly regarding the specific pathways and genes involved. Additionally, more research is required to outline the specific roles of endogenous melatonin and NO as well as the effects of various stressors on their interactions. Finally, identifying novel melatonin and NO receptors and downstream signaling pathways may provide insights into their interactions and mechanisms of action, ultimately leading to the development of new strategies for improving plant stress tolerance.

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9

Diverse Functional Role of Melatonin in Postharvest Biology

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Abstract

A new biomolecule called melatonin (*N*-acetyl-5-methoxytryptamine) affects the growth of horticultural crops both before and after harvest. The most important role of melatonin in higher plants is an indoleamine neurotransmitter and antioxidant that can regulate reactive oxygen and nitrogen species. It is a signalling agent that induces various specific physiological activities in plants that might serve to increase growth, photosynthesis, root initiation, fixation of carbon, defence, and germination of seed against various abiotic and biotic stressors. However, its role in postharvest biology bears significant potential in improving quality, fruit ripening, shelf life, postharvest preservation, and stress protection (biotic as well as abiotic stress) during storage. Recent studies on postharvest biology of horticultural crops revealed the role of melatonin in preventing senescence, antioxidant action, etc. which are very important with respect to economic value of horticultural commodities. The positive influence of melatonin on postharvest biology is utilised in shelf life extension and quality retention in terms of sensorial and nutritional quality. It is now well evident that the addition of melatonin enhances the postharvest biology of various horticultural crops. Additionally, many new aspects have been identified where melatonin may have possible roles in reduction in the pesticide residues accumulation and heavy metals in foods. The detailed information on the diverse functional role of melatonin in postharvest biology, viz. its importance in postharvest management, signalling, regulation, application in horticultural crops, etc. are discussed in detail in this chapter.

Keywords

Melatonin · Postharvest preservation · Biotic and biotic stress · Antioxidant

9.1 Introduction

Melatonin is a pleiotropic substance that affects broad range of cellular and physiological actions in several kingdoms (Arnao and Hernandez-Ruiz 2015). It functions as a neurohormone and is secreted by the pineal gland into the bloodstream and cerebrospinal fluid. It is discovered in the bovine pineal gland and was given that name by Aaron Lerner and his co-workers in 1958. The first-time melatonin was found in plants was in 1995. Since then, it has been reported in a several species of plants and their different tissue parts, including strawberry, cucumber, tomato, grape, pepper, rice, apple, wheat, and solanaceous, etc. (Li et al. 2023). This indoleamine has a crucial role in the regulation of a number of physiological processes, including circadian rhythms, sleep, retinal physiology, mood, appetite, body temperature, sexual behaviour, and the immune system (Yang et al. 2022). The duration as well as the timing of the melatonin signal have therefore revealed a function in photoperiodic control.

The enzymes tryptophan decarboxylase, 5-hydroxytryptamine-*N*-acetyltransferase, 5-hydroxytryptamine-*N*-methyltransferase, and *N*-acetyl-5-hydroxytryptamine-methyltransferase catalyse the synthesis of melatonin from tryptophan, which is further catabolised to 2-hydroxymelatonin by the action of melatonin 2-hydroxylase (Rui et al. 2016; Arnao and Hernandez-Ruiz 2021). In plants, melatonin is generally synthesised in the chloroplasts and mitochondria of leaves and/or roots before being transmitted to meristems, flowers and fruits, whereas, in vertebrates, it is primarily produced in the pineal gland and then secreted rhythmically into the bloodstream after it has been produced (Nawaz et al. 2020). It plays a crucial role in a wide range of biological process in plant species, such as circadian rhythm, photo-response regulation, senescence of leaves, seed germination, and rooting. In addition, it has been revealed how melatonin regulates gene expression and its interactions with other phytohormones such as auxin, gibberellic acid (GA), cytokinin, (Abscisic acid) ABA, ethylene, and salicylic acid (Xu et al. 2019). It is a potent antioxidant and free radical scavenger agent that protects proteins and membrane lipids from free radical damage (Li et al. 2023). Several vegetables and fruits, such as peaches, cassava, bananas, mangoes, and cucumber have been reported to have strong antioxidants properties (Prasad et al. 2016, 2020) and contain melatonin, suggesting that it has a significant role in postharvest biology (Li et al. 2023).

In recent time, the most advantageous impact of melatonin on postharvest biology are utilised in extension of shelf life and better-quality retention in terms of sensorial and nutritional quality. It is now well evident that the addition of melatonin to various fruits and vegetables enhance the postharvest life hence maintaining their nutritional qualities. Additionally, many new aspects have been identified where melatonin may have possible roles in reduction in the pesticide residues accumulation and heavy metals in foods. The detailed information on the diverse functional role of melatonin in postharvest biology, viz. its importance in postharvest management, signalling, regulation, application in horticultural crops, etc. are highlighted in detail in this chapter.

9.2 Role of Melatonin in Postharvest Management

9.2.1 Postharvest Losses in Fruit and Vegetables

The postharvest losses occur approximately 20–40% in various fruits and vegetables (Prasad et al. 2018a), which takes place at several stages of postharvest handling, i.e., fruit characteristics (Saroj and Prasad 2023), harvesting (Prasad et al. 2019), transportation, storage (Prasad et al. 2016), and marketing (Prasad et al. 2018a, 2022a). Therefore, it is crucial to use postharvest management techniques that are both effective and efficient when managing fresh horticultural produce (Prasad et al. 2022a, b). These include proper harvesting method (Prasad et al. 2019), pre-cooling, sorting, grading, packaging, and storage (Prasad and Sharma 2018; Prasad et al. 2022b). Many postharvest techniques have been proposed to mitigate chilling injury, physiological disorders (Prasad and Sharma 2016), minimising decay

(Prasad et al. 2016) thereby control ripening which ultimately enhance shelf life of the produce (Prasad and Sharma 2018; Prasad et al. 2018b; Jayarajan and Sharma 2021).

9.2.2 Melatonin Role in Postharvest Management of Fruit and Vegetables

Melatonin appears to have a potential involvement in the postharvest management of fruits and vegetables, as well as in alleviating biotic and abiotic stresses. Some other novel molecules also have demonstrated their ability in the postharvest management of various fruits and vegetables, including nitric oxide (NO), 1-MCP, salicylic acid (SA), and brassinosteroids (BRs) (Prasad et al. 2018b).

9.2.3 Role of Melatonin in Alleviation of Chilling Injury

The shelf life of postharvest vegetables and fruits can be enhanced by low temperature storage (Prasad et al. 2018b). However, chilling injury during low temperature storage may occur in various horticultural crops, lowering the flavour and quality of the produce (Prasad et al. 2022b). Recent research has shown that exogenous melatonin treatment enhances chilling tolerance and reduces chilling injury in various fruits and vegetables at the time of cold storage such as peaches, tomatoes, pomegranates, and sapotas (Ze et al. 2021; Jayarajan and Sharma 2021) (Table 9.1). The chilling injury index in plums is reduced by pre-treatment with 0.1 mM melatonin (Bal 2019; Du et al. 2021). It has been observed that external application of melatonin reduced malondialdehyde (MDA) content, leakage of electrolyte as well as lipoxygenase activity of postharvest fruit during low temperature storage (Jayarajan and Sharma 2021). However, fruit firmness changes in distinct ways following various melatonin treatments. For instance, a 10-min treatment with 0.1 mM melatonin greatly improved the firmness, melatonin increases the synthesis of polyamines in the treated product (Gao et al. 2018; Molla et al. 2022). The genes and essential polyamine production enzymes including ornithine decarboxylase and arginine decarboxylase were controlled by treatment of melatonin. Similarly, the expression of PpADC, PpGAD, PpODC, and genes that enhanced the content of polyamines and γ-aminobutyric acid (GABA) also improved by melatonin treatment (Jayarajan and Sharma 2021). The melatonin treatment resultant in the production of unsaturated fatty acids which reduced the harmful effects of chilling injury in green bell peppers, peach, and also played a significant role in reducing the chilling injury of banana, when fruits were stored in low temperature (Wang et al. 2021; Ze et al. 2021) (Table 9.1). Treatment of ‘Baitangying’ litchi fruit with 400 μM melatonin has shown promising results in preventing discoloration, possibly by limiting the increase in malondialdehyde (MDA) content and the occurrence of chilling injury. These effects may be attributed to an improvement in the integrity of the cell membranes (Gao et al. 2022). Treating pomegranate fruits with 100 μM melatonin

Table 9.1 Effect of melatonin on chilling injury various horticultural crops

Fruit/ vegetable	Melatonin concentration (μM)	Impact	References
Pear	100	Enhanced chilling tolerance	Jayarajan and Sharma (2021)
Plum	100	Significant increase in chilling tolerance in stored plums	Bal (2019), Du et al. (2021)
Bell pepper	100	Melatonin treatment reduced chilling injury by reducing the peroxidation of membrane lipids and by triggering the antioxidant defence system.	Wang et al. (2021)
Strawberry	100	Increased tolerance in treated fruits	Jayarajan and Sharma (2021)
Tomato	100	Enhanced tolerance against chilling injury, upregulation of ZAT2/6/12 resulted in more synthesis of nitric oxide, polyamine, and proline	Jayarajan and Sharma (2021)
Sapota	90	Alleviation of chilling injury, decreased leakage of electrolytes, superoxide anion, and MDA content as well as higher antioxidant defence mechanism	Mirshekari et al. (2020)
Pomegranate	100	Chilling injury alleviation, increased integrity of membrane, reduced production of peroxidases, and as well as increased antioxidant enzymes activities	Aghdam et al. (2020)
Peach	100	Tolerance against chilling injury which might be due to the increased levels of proline and GABA due to enhanced expression of PpADC, PpODC, and PpGAD genes	Ze et al. (2021)
Cherry	100	Reduced fruit decay	Wang et al. (2019a, b)

ADC arginine decarboxylase, *MDA* malondialdehyde

leads to a reduction in peroxidase production, which subsequently results in enhanced activities of ROS scavenging enzymes such as catalase, ascorbate peroxidase, glutathione reductase, and superoxide dismutase. This overall increase in antioxidant enzyme activity contributes to an improvement in the membrane integrity of the pomegranate fruits (Aghdam et al. 2020) (Table 9.1).

9.2.4 Role of Melatonin in Postharvest Disease Control

Recently, there has been a lot of interest in finding alternative, safe, and effective disease prevention methods (Prasad et al. 2022a, b). Application of melatonin to immature cucumber greatly reduced the sporulation intensity and diameter of the lesions. Treatment with 100 μM melatonin decreased the disease index of ginger rhizome rot caused by *P. brevicompactum* and *F. oxysporum*, two significant postharvest decay fungi (Huang et al. 2021). Cherry tomatoes were soaked for 60 min in 100 μM melatonin and then kept at 22 ± 1 °C to dramatically prevent the growth of grey mould brought on by *Botrytis cinerea*'s effects on the phenylpropanoid pathway. These findings suggest that melatonin treatment may be used as an environmentally friendly biocontrol strategy to control the postharvest diseases (Gao et al. 2022).

9.2.5 Role of Melatonin Delay in Ripening and Senescence

Although the terms 'ripening' and 'senescence' are frequently used interchangeably, ripening is an active, genetically controlled process by which fruit gets ready for the biochemical and molecular changes needed in the final stages of development that result into senescence, which includes deteriorating changes and disorders (Wang et al. 2020). Several studies have showed the melatonin role in controlling fruit ripening and senescence after harvest, particularly for climacteric fruits. Production of ethylene in apples during postharvest storage was reduced after treatment with melatonin (Jayarajan and Sharma 2021) (Table 9.2). Various fruit quality characteristics, such as carotenes, respiration rate, titratable acidity, organic acids, weight loss, soluble sugars, and volatile aroma, can be maintained greatly after melatonin treatment. For instance, in cherry, mango, and banana, melatonin treatment significantly reduced the increase of TSS which reduces the fruit ripening (Ze et al. 2021). Postharvest ripening in banana delayed by melatonin treatment and this effect was dependent on concentration (200 and 500 μM were more effective than 50 Mm) (Gao et al. 2022) (Table 9.1). The ethylene production also reduced by exogenous melatonin application by regulating the expression of MaACO1 and MaACS1 (Jayarajan and Sharma 2021). Ethylene and melatonin, however, do not always work together during the postharvest fruits ripening process. For example, ethylene production of tomato fruit was positively influenced by 50 μM melatonin, which promoted its ripening resulting in changes of biochemical processes such as accumulation of pigments (lycopene and carotenoid), degradation of cell wall and biosynthesis of various volatile compounds (Sun et al. 2020). The very complex interaction between melatonin and ethylene or the postharvest temperature may be responsible for this outcome. Melatonin at a concentration of 100 μM significantly raised ABA and H_2O_2 levels, increased ethylene production, and accelerated ripening of 'Moldova' grape berries. A better understanding of melatonin signalling during grape berry ripening was thus made possible by the indirect role that melatonin plays in ripening through the modulation of ABA signalling (Jayarajan and Sharma 2021).

Unlike fruit ripening, which involves a series of physiological and biochemical changes leading to fruit maturation, fruit senescence refers to the gradual deterioration of fruit quality over time. During senescence, the tissue structure and nutritional

Table 9.2 Effect of melatonin treatment on ripening and delay in senescence in fruits and vegetables

Fruit	Melatonin concentration	Impact	References
Grape	100 μM for 5 s	Increase ripening, total soluble solids, and anthocyanin content	Jayarajan and Sharma (2021)
Broccoli	1 μM	Reduced postharvest senescence, and retained levels of antioxidants, including glucosinolates, vitamin C, and total phenols	Jayarajan and Sharma (2021)
Mango	1 mM for 10 min	Delayed ripening, senescence and enhance ascorbic acid and phenolics, flavonoids	Rastegar et al. (2020)
	500 μM for 1 h	Delayed ripening, β-carotene, and total soluble solids (TSS)	Ze et al. (2021)
Tomato	50 μM	By increasing the expression of the gene for colour development and ethylene generation, they accelerated ripening and extended postharvest shelf life. Promoted carotenoid synthesis	Sun et al. (2020)
Cherry	100 μM	Reduced respiration to delay senescence	Wang et al. (2019a, b)
Kiwifruit	150 μM	Improved shelf life and postponed senescence	Jayarajan and Sharma (2021)
Banana	50, 200, 500 μM for 2 h	Delayed ripening by reducing ethylene production	Gao et al. (2022)
Apple	1 mmol L^{-1}	Lowered ethylene production and delayed senescence	Jayarajan and Sharma (2021)
Peach	100 μM for 10 min	Reduced decay, senescence and maintained higher ascorbic acid and phenolics, TSS	Ze et al. (2021)
Litchi	400 μM for 5 min	Delayed senescence	Zhang et al. (2018) and Ze et al. (2021)
Sweet cherry	100 μM	Delayed senescence	Xia et al. (2020)

components of the fruit steadily degrade, leading to a decline in overall fruit quality. It has been observed that the senescence of postharvest produce significantly delayed by exogenous melatonin treatment and, thus, extended the shelf life (Ze et al. 2021). Fruit firmness is maintained by melatonin treatment by delaying cell wall degradation (Wang et al. 2019b). By using 200 μM melatonin, 'Kyoho' grapes experienced reductions in rot index and berry shedding of 37.50% and 58.37%, respectively. The application of melatonin at a concentration of 100 μM has a positive effect on delaying yellowing in broccoli (*Brassica oleracea* var. italica) during storage. The specific mechanisms behind this delay are related to the preservation of chloroplasts and the inhibition of chlorophyll catabolic enzymes (Gao et al. 2022) (Table 9.2). The activities of cellulose, pectin methylesterase, polygalacturonase, and glucosidase were all inhibited by melatonin, which further delayed the softening of ber

(*Ziziphus jujuba* Mill.) (Sun et al. 2022). Application of melatonin at a concentration of 400 μM in litchi fruits (*Litchi chinensis* Sonn. cultivar 'A4Wuhe') has beneficial effects in preventing pericarp browning and delaying postharvest fruit senescence. The positive outcomes are attributed to two key factors: the inhibition of cell wall-degrading enzymes and the enhancement of energy metabolism (Wang et al. 2020; Gao et al. 2022).

9.2.6 Role of Melatonin in Shelf Life and Fruit Quality

Melatonin has shown promising effects in enhancing the quality of horticultural crops and their products by enhancing the content of various advantageous attributes. Several studies have demonstrated that exogenous melatonin treatment can lead to an increase in natural antioxidants, phenolics, sucrose, polyphenols, soluble solids, and aroma components in different fruits such as grapes, pomegranate, jujubes, and sweet cherry (Wang et al. 2021; Jayarajan and Sharma 2021). In grapes, the concentration of specific compounds like cyanin-3-*O*-glucoside, peonidin derivatives, catechins, epicatechins, flavanols, and their derivatives increased after melatonin treatment. Treatment with melatonin during the maturation of grape berries increased the flavonoid 3′-hydroxylase activity and/or VvF3′ H gene expression. The significance of postharvest melatonin application for enhanced quality and postponed senescence in sweet cherries was observed and discussed by Wang et al. (2019a). In an experiment, freshly harvested sweet cherries were given treatments containing different melatonin concentrations (50, 100, 150 μM/L). It was found that the 100 μM/L melatonin treatment effectively reduced decay incidence and weight loss and maintained TSS, TA, better firmness and delaying the process of senescence (Jayarajan and Sharma 2021) (Table 9.3). Melatonin application offers multiple benefits in terms of improving the antioxidant defence system in plants (Fig. 9.1). Apart from limiting the generation of oxygen radicals, melatonin has been shown to enhance the activity of various antioxidant enzymes such as SOD, CAT and increase the content of essential antioxidants like Ascorbic acid (AsA) and Glutathione (GSH) In litchi, it also postponed senescence (Zhang et al. 2018) (Table 9.3).

Melatonin is used after harvest to extend the shelf life of a variety of fruits and vegetables, including bamboo (*Phyllostachys edulis*) shoots, broccoli (*Brassica oleracea* L.), peaches (*Amygdalus persica* L.), pomegranates (*Punica granatum* L.), and tomatoes by acting as an antioxidant by scavenging reactive oxygen species (ROS) which are generated in cold storage (Wu et al. 2021). Similar to this, applying exogenous melatonin to apple juice can prolong its shelf life, boost antimicrobial activity, and prevent browning (Xu et al. 2019). Additionally, it increased the amount of total phenols and anthocyanins in strawberry and litchi, preserving the fruit's nutritional value (Wang et al. 2020).

Table 9.3 Effect of melatonin treatment on shelf life and quality of fruits in fruits and vegetables

Fruit	Melatonin concentration	Impact	References
Apple	1 mmol L^{-1}	'Fuji' apples' postharvest quality was preserved, and during storage, weight loss and peel damage were decreased.	Jayarajan and Sharma (2021)
Pear	100 µM	Delayed senescence, enhanced firmness, and AOX activities to prolong shelf life.	Ze et al. (2021), Zhai et al. (2018)
Nectarine	500 and 1000 µmol L^{-1}	Extended shelf life of fruits, maintained the appearance and nutrient value, and the loss of chemicals that promote health was decreased.	Bal (2020, 2021)
Cherry	100 µM	Maintained better firmness, TSS, TA by lowering rate of respiration and delaying senescence.	Wang et al. (2019a, b)
Jujube	100 µM	Delayed fruit discolouration and increased accumulation of phenolic compounds.	Wang et al. (2021)
Strawberry	100 µM	Maintained higher total antioxidant, phenolic compounds and enhanced the activities of various antioxidants enzymes.	Ze et al. (2021)
Pomegranate	100 µM	Increased PAL activity resulted in higher phenols and anthocyanin accumulation. Increased PAL activity, phenolics and reduced PPO activity.	Aghdam et al. (2020), Jayarajan and Sharma (2021)

AOX alternative oxidase, *TSS* total soluble solids, *TA* titratable acidity, *PAL* phenylalanine ammonia-lyase, *PPO* polyphenol oxidase

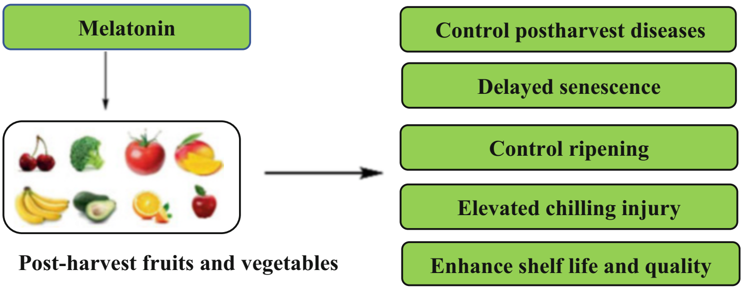

Fig. 9.1 Effect of melatonin on postharvest management of horticultural crops

9.3 Melatonin Signalling and Regulation of Postharvest Biology

9.3.1 Melatonin Mediated Signalling

Plant development and stress resistance are both significantly influenced by melatonin (Zhang et al. 2022). Biosynthesis of melatonin in higher plants can be induced in response to various abiotic stresses, such as drought, cold, and exposure to heavy metals. These stressors can trigger specific signalling pathways that lead to the activation of stress response factors, which in turn promote the synthesis of melatonin (Park and Back 2012; Zhang et al. 2022). The signalling pathway for melatonin in plants has been a subject of research interest. One significant finding was the identification of the candidate G protein coupled receptor 2 (CAND2) as the first Phytomelatonin receptor identified in *Arabidopsis thaliana* (Wei et al. 2018; Sun et al. 2023). By encouraging the CAND2 receptor and heterotrimeric G protein subunit (GPA1) connected to CAND2, exogenous melatonin application at a 50 μM concentration elevated the RNA polymerase genes RPOTm and RPOTmp. The exogenous melatonin application at a concentration of 50 μM can have specific effects on gene expression in plants. These effects are related to the CAND2 receptor and its interaction with the heterotrimeric G protein subunit GPA1 and led to an increase in the expression of two RNA polymerase genes, i.e., RPOTm and RPOTmp (Zhang et al. 2022; Bychkov et al. 2022). In *Arabidopsis thaliana*, the CAND2/PMRT1 (Candidate 2/Phytomelatonin Receptor 1) receptor has been identified as a membrane protein found on the plasma membrane. CAND2/PMRT1 interacts with GPA1, a heterotrimeric G protein subunit, and plays a role in regulating stomatal movement via the ROS signalling pathway, which is controlled by NADPH oxidase (Li et al. 2020; Zhang et al. 2022). Through upstream MAPK kinases (MKKs), such as MAPKK4, MAPKK5, MAPKK7, and MAPKK9, treatment with 1 M melatonin activated MAPK3 and MAPK6 (Zhang et al. 2022). An Arabidopsis knockout mutant (agb1)'s G protein levels did not alter, proving that the activation was unrelated to G protein signalling (Fig. 9.2). This demonstrated that various MAPKK/MAPK components sent MAPK signals that promoted innate immunity in response to melatonin. According to Chisholm et al. (2006), PAMP-triggered immunity (PTI) and effector-triggered immunity (ETI) are activated as a result of the activation of MEKK, which is thought to be mediated by melatonin receptors or receptor kinases that recognise PAMPs (pathogen-derived molecular patterns) and effectors. Melatonin causes plant responses by activating MAPKKK3 and oxidative signal-inducible 1 (OXI1) (Lee and Back 2017).

9.3.2 Effects of Melatonin on Postharvest Biology

Melatonin has been demonstrated to possess exceptional antioxidant properties in humans, animals, and higher plants both in vivo and in vitro. Along with removing reactive oxygen species (ROS) from plants, melatonin also induces antioxidant

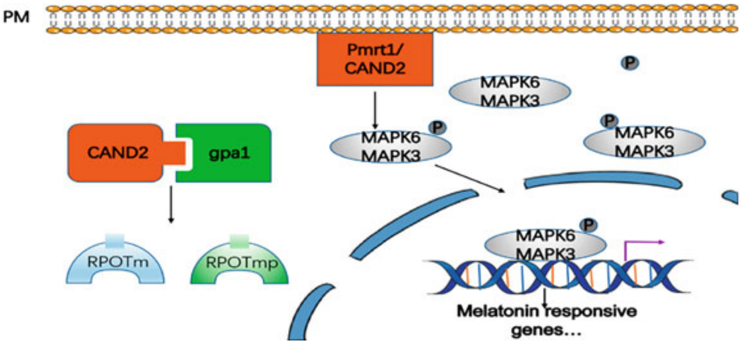

Fig. 9.2 From melatonin perception to action, the melatonin signalling route. The production of melatonin's receptor protein is stimulated, allowing upstream MKK to activate MAPK3 and MAPK6, which in turn activates melatonin. G protein coupled receptor 2 (CAND2); mitogen associated proteinase kinase; RPOTm: RNA polymerase of the mitochondria

defence mechanism by increasing gene expression (Wang et al. 2020; Zhang et al. 2020). Melatonin delayed the senescence of horticultural crops by suppressing the biosynthesis of ABF-mediated abscisic acid (ABA), degradation of chlorophyll, controlling the lipid and energy metabolism in membranes, preventing biosynthesis of ethylene via regulation of nitric oxide, enhancing the content of ascorbic acid and total phenols (Wu et al. 2021).

Additionally, the signal molecule melatonin can regulate a number of physiological functions in higher plants (Liu et al. 2020; Wang et al. 2020). The postharvest ripening of a number of fruits, including banana, sweet cherry, kiwifruit, and mango was considerably slowed down by exogenous melatonin application (Ze et al. 2021). Exogenous melatonin application during storage, such as with bananas (Li et al. 2019), sweet cherry (Wang et al. 2019a), peach (Gao et al. 2016), and pear (Liu et al. 2019) also considerably slowed down senescence and the breakdown of postharvest fruit. When strawberries are treated with exogenous melatonin, they are significantly more resistant to cold when kept at low temperatures. As a result, chilling injury of postharvest fruits like tomato, peach (Wang et al. 2020), pomegranate (Jannatizadeh 2019), and sapota (Mirshekari et al. 2020) gets reduced. External application of melatonin can also considerably increase disease resistance and reduce deterioration in a variety of stored fruits, such as kiwifruit, strawberries, peaches, and plums (Ze et al. 2021).

9.4 Conclusion

The reviewed literature underscores the crucial role of melatonin in postharvest biology, presenting it as a pivotal tool for enhancing the storage and overall quality of agricultural produce. One of the key factors that make melatonin highly valuable in this context is its potent antioxidant properties. By acting as an effective scavenger of harmful free radicals, melatonin shields plants from oxidative stress induced by biotic factors like pathogens and abiotic factors such as extreme temperatures and irradiation. This vital attribute of melatonin significantly reduces the susceptibility of horticultural crops to various stressors during postharvest handling and storage, thus preserving their freshness and nutritional value. Among the major postharvest challenges faced by the agricultural industry, chilling injury and decay stand out as significant threats to crop quality and marketability. However, the application of exogenous melatonin offers a promising solution. By treating crops with melatonin, chilling injury symptoms can be mitigated, especially in temperature-sensitive varieties. Furthermore, melatonin's antimicrobial properties play a critical role in inhibiting decay-causing microorganisms, ensuring better storage longevity and reducing postharvest losses. Another remarkable aspect of melatonin's influence on postharvest biology is its ability to regulate ripening and delay senescence in various horticultural crops. Through the ripening regulation melatonin prolongs the shelf life of produce while maintaining quality during transportation and storage. This controlled ripening process also contributes to improved taste, colour, and texture, enhancing consumer satisfaction and marketability.

Beyond its direct benefits to postharvest management, melatonin offers substantial advantages to the broader context of sustainable agriculture. Being a biodegradable and non-toxic compound, melatonin aligns perfectly with organic farming practices, providing an environmentally friendly alternative to synthetic chemicals. Its application in organic agriculture not only enhances the quality and shelf life of organic produce but also supports the industry's commitment to ecologically sound and health-conscious farming practices. In conclusion, the reviewed literature presents melatonin as a crucial player in postharvest biology, offering a range of benefits that contribute to the improved storage, extended shelf life, and enhanced quality of horticultural crops. Its antioxidant properties protect plants from stressors, while its ability to regulate ripening and senescence ensures optimal produce conditions. Furthermore, as a biodegradable and non-toxic compound, melatonin's potential to support organic farming practices adds to its appeal as an eco-friendly and sustainable solution for the agricultural industry.

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Regulatory Role of Melatonin in Post-harvest Management of Vegetables and Fruits

10

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Abstract

In nature, melatonin is widely distributed, and not only does it play a vital role for animals and humans, but also for plants. Plants use melatonin for a wide range of purposes, including preventing senescence, acting as an antioxidant, regulating growth and development, and adjusting to stressful conditions. Fruits and vegetables contain it naturally, and its presence greatly influences the ripening and post-harvest processes. As a result of increasing the activity of antioxidant enzymes, non-enzymatic antioxidants, and enzymes involved in repairing oxidized proteins, melatonin is effective in reducing reactive oxygen species levels in post-harvest fruits and vegetables. Exogenous melatonin can also increase endogenous melatonin levels, enhancing its effects on a variety of physiological processes. Exogenous melatonin has been shown to improve the post-harvest preservation of fruits and vegetables in several studies. While

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transgenic methods could potentially be used to overproduce melatonin in plants and improve post-harvest preservation, current attempts are limited to increasing endogenous melatonin in plants. Recent advances in understanding melatonin's role and mechanisms in post-harvest fruits and vegetables are summarized in this review. Additionally, it provides insights into future approaches to maximizing fruit and vegetable preservation post-harvest. Research in this area could lead to innovative strategies for reducing food losses and improving the quality of fruits and vegetables after harvest.

Keywords

Melatonin · Post-harvest · Fruits · Vegetables · Preservation

10.1 Introduction

Agricultural research in developing countries focuses primarily on enhancing the productivity and production of cereals. As a first point, cereals are a valuable source of affordable and accessible food for economically disadvantaged people. Additionally, cereals contain a range of essential nutrients, including carbohydrates, proteins, lipids, micronutrients, vitamins, phenols, and antioxidants. With a projected nine billion population by 2050, agriculture will be under tremendous pressure to meet the increased demand for food as a result of this population growth. In order to ensure food security for the growing global population, researchers and policymakers need to find sustainable and efficient ways to increase agricultural productivity (Hubert et al. 2010; Yadav et al. 2023; Jaiswal et al. 2023a; Mandal et al. 2023a). Agriculture and related fields have been successful in meeting the food and feed needs of the impoverished population in developing countries thanks to modern technology. In these countries, research and development have mainly focused on increasing food production, often neglecting nutritional value in the process. The focus must shift now to enhancing food production as well as nutritional quality (Komatsu et al. 2019; Thakur et al. 2023a; Tiwari et al. 2023). The production of food and feed is essential, but it must be done while preserving the agroecosystem in order to maintain a delicate balance. Micronutrient undernourishment is one of the biggest challenges facing the world, particularly in developing countries (Ortiz-Monasterio et al. 2007). Rice, wheat, and maize are important staples in these regions because they provide vitamins and minerals. In addition to being rich in carbohydrates, these foods are also deficient in vitamins and minerals. Humans require relatively small quantities of macroelements and trace amounts of microelements, including iron, copper, zinc, iodine, and selenium, along with substantial amounts of carbohydrates, proteins, and lipids, in order to maintain a healthy lifestyle (Welch 2002; Kumar et al. 2023a; Mandal et al. 2023b; Raza et al. 2023). Therefore, it is essential to address this issue and ensure that food production not only increases but also focuses on providing better nutritional content to combat micronutrient deficiencies.

Several characteristics and properties make fruits and vegetables valuable for human consumption. Growers and shippers need to ensure their produce has a pleasing appearance and minimal visual defects in order to determine the quality of their product. These characteristics include appearance, texture, flavor, and nutritive value (Brandão et al. 2021; Li et al. 2023b; Zhao et al. 2023; Lin et al. 2023). In addition, they prioritize cultivars that are useful for yield, disease resistance, harvest ease, and shipping. These characteristics have often been given more importance by plant breeders than flavor and nutritional value (Shewry and Hey 2015; Mangal et al. 2022; Thakur et al. 2023b; Verma et al. 2023). Meanwhile, receivers and market distributors place a high value on the quality of their fruits and vegetables. They are also keenly interested in firmness and how long the produce can be stored. Research into post-harvest biology and technology has traditionally focused primarily on quality evaluation based on appearance and texture (Brasil and Siddiqui 2018; Singh et al. 2022; Jaiswal et al. 2023b; Jeevalatha et al. 2023). Although grains and seeds are commonly used as food preparation ingredients, they contain low levels of micronutrients, and the nutrients that are present may be highly bioavailable. In order to address the widespread issue of micronutrient undernourishment affecting over half of the world's population, improvements are needed to increase the uptake efficiency of micronutrients and vitamins, making them more bioavailable (Sanahuja et al. 2013). There is a notable deficiency of vitamins and minerals in staple foods in developing countries, a significant portion of the population relying on them (Ortiz-Monasterio et al. 2007; Mandal et al. 2023b; Buttar et al. 2023; Lal et al. 2023a).

There are a series of changes in physiology, biochemistry, and metabolism that occur as a result of fruit and vegetable senescence, which is an irreversible process. As this process unfolds, the color, flavor, and nutritional content of the produce decline, resulting in a reduction in shelf life (Prasanna et al. 2007; Singh et al. 2023; Jia et al. 2023; Zhao et al. 2023). In fruits and vegetables, post-harvest decay occurs primarily as a consequence of continuous respiration, which depletes their own nutrients, causing chlorophyll degradation, substrate oxidation, softening of cell walls, and membrane permeability. The nutritional changes during storage are also affected by factors such as temperature, humidity, and air composition (Barrett and Lloyd 2012; Sharma et al. 2023b; Kumar et al. 2023a; Devi et al. 2023). Various traditional physical storage methods have been developed to extend the storage period of fruits and vegetables after harvest, including refrigeration, controlled atmosphere storage, and ventilation storage (Yousuf and Qadri 2019; Ramos et al. 2020).

As a widely distributed biomolecule with diverse effects, melatonin has been studied extensively in different biological systems, from tiny microbes such as bacteria, to complex systems like humans, animals, and plants. In different biological systems, it plays a major role in regulating circadian rhythms and biological cycles in plants and animals (Stehle et al. 2011; Rather et al. 2022; Thakur et al. 2023a; Sharma et al. 2023b). *N*-acetyl-5-methoxytryptamine is melatonin's chemical name, an indoleamine that shares structural similarities with other indoleamines such as tryptophan, auxin, and serotonin. Interestingly, melatonin shares a common precursor with auxins, and its biosynthetic pathway is similar to that of auxins (Murch et al. 2000; Mangal et al. 2023; Wang et al. 2023; Kumar et al. 2023b). There are a number of crucial roles melatonin plays in animals, including sleep, mood, retinal function, sexual behavior, immune response, and circadian rhythm. The pleiotropic effects of melatonin make it an essential biomolecule with many functions in living systems. It has been extensively studied and confirmed by researchers worldwide (Zhao et al. 2019; Tiwari et al. 2021, 2022a, b; Altaf et al. 2022b, 2023a, b). In addition to humans, melatonin has been discovered in edible plants belonging to both monocotyledonous and dicotyledonous families in 1995 (Dubbels et al. 1995; Hattori and Taylor 2009). A series of enzyme reactions involving tryptophan decarboxylase, tryptamine-5 hydroxylase, 5-hydroxytryptamine-*N*-acetyltransferase, and *N*-acetyl-5 hydroxytryptamine-methyl transferase are involved in the production of melatonin in plants. As a result, melatonin 2-hydroxylase catabolizes it to 2-hydroxymelatonin (Tan et al. 2013; Xia et al. 2021). After being synthesized in mitochondria and chloroplasts of leaves and/or roots, melatonin is transported to flowers, fruits, and meristems in plants (Arnao and Hernández-Ruiz 2013). A number of biological processes are affected by melatonin in plants. As well as regulating circadian rhythm and photo-response, it influences leaf senescence (Dhindsa et al. 1981; Altaf et al. 2023a; Lal et al. 2023b; Rahman et al. 2023), and promotes seed germination and root growth (Zhang et al. 2013). A number of phytohormones interact with melatonin, including auxin, cytokinin, gibberellins, abscisic acid, ethylene, jasmonic acid, and salicylic acid, according to recent research. These phytohormones have been shown to modulate gene expression using melatonin, as a result, melatonin plays a diverse and intricate role in plant physiology and has the potential to regulate many plant processes (Altaf et al. 2021a, 2022c; Saqib et al. 2022).

The aim of the review is to provide valuable insights for the future integration of melatonin and ROS as signal molecules in the field of fruit and vegetable preservation. Furthermore, the review emphasizes the importance of ROS signaling in these processes. Fruit and vegetable senescence is regulated by reactive oxygen species, which have a major role to play in post-harvest physiology (Altaf et al. 2022a; More et al. 2023; Kumar et al. 2023c; Mukherjee et al. 2023; Choudhary et al. 2023). Melatonin interacts with ROS signaling in the review, potentially affecting preservation. In order to serve as a valuable reference for future research and the development of sophisticated preservation strategies integrating both melatonin and ROS as signal molecules, this chapter provides a comprehensive understanding of the interactions between melatonin and ROS, as well as their roles in fruit and vegetable preservation. In this way, fruit and vegetables could be processed in a sustainable and efficient manner, thus improving their post-harvest quality.

10.2 Role of Melatonin in Plant and Post-harvest Physiology

In plants, melatonin plays a pleiotropic role ranging from seed germination to propagation to senescence. It is widely distributed both in plants and in animals. In addition to acting as a potent antioxidant, it can move freely throughout the plant system in both aqueous and fat-soluble environments (Nawaz et al. 2016; Yadav et al. 2022; Altaf et al. 2022a; Sharma et al. 2023a). In fruit and vegetable plants, melatonin plays a significant role in various aspects. It is involved in seed germination, growth, and development. Moreover, melatonin can provide a wide range of tolerance to both biotic and abiotic stresses in standing crops and after harvest. Studies have shown that it can alleviate biotic stresses caused by pests and diseases as well as abiotic stresses caused by temperature extremes, salinity, and drought (Arnao and Hernández-Ruiz 2014; Moustafa-Farag et al. 2020; Tiwari et al. 2022a). In the post-harvest stage, the application of melatonin as a treatment has shown promise in mitigating various stresses. In particular, it has been used to combat chilling injury, control decay, and delay senescence, extending fruit and vegetable post-harvest life and reducing losses (Uchendu et al. 2013; Bose and Howlader 2020). Even though this application is relatively new, the potential benefits of using melatonin in post-harvest treatments are becoming increasingly evident and hold promise for improving fruit and vegetable quality and preservation (Xu et al. 2019a; Jayarajan and Sharma 2021; Li et al. 2023a).

As a source of essential nutrients, fruits and vegetables play a crucial role in maintaining a healthy diet, including vitamins, minerals, phenols, and fibers (Kumar et al. 2020d; Lal et al. 2020a, b, c; Alegbeleye et al. 2022). As a result, increasing the consumption of fruits and vegetables can reduce the risk of cardiovascular disease and certain chronic illnesses, while also increasing the body's antioxidant and anti-inflammatory capabilities (Boeing et al. 2012; Maheshwari et al. 2022). These foods, for instance, contain polyphenols that inhibit multiple inflammation-associated cell signaling pathways, effectively inhibiting chronic inflammation. Fruits and vegetables, however, face one of the greatest challenges after harvest: post-harvest losses. A number of factors contribute to these losses, including mechanical damage, water and phytochemical loss, and microbial infection, all of which become problematic during long-term storage (Salehi 2020; Barbhuiya et al. 2022). A variety of storage technologies are employed to reduce post-harvest losses, including cold chain management, hypobaric storage, modified atmosphere packaging (MAP), and ultraviolet treatment. Fruits and vegetables can also be preserved with natural or synthetic preservatives, but this method can leave chemical residues behind (Valencia-Chamorro et al. 2011; Tarangini et al. 2022). According to recent studies, plant natural hormones such as melatonin, ethylene (ET), salicylic acid (SA), and methyl jasmonate (MeJA), together with signaling molecules like nitric oxide (NO), hydrogen sulfide (H_2S), and reactive oxygen species (ROS), regulate fruit and vegetable maturation and senescence (Altaf et al. 2020, 2021b, 2022d). As a result of these natural compounds, perishable items can have their shelf life prolonged and post-harvest senescence delayed (Li et al. 2023b).

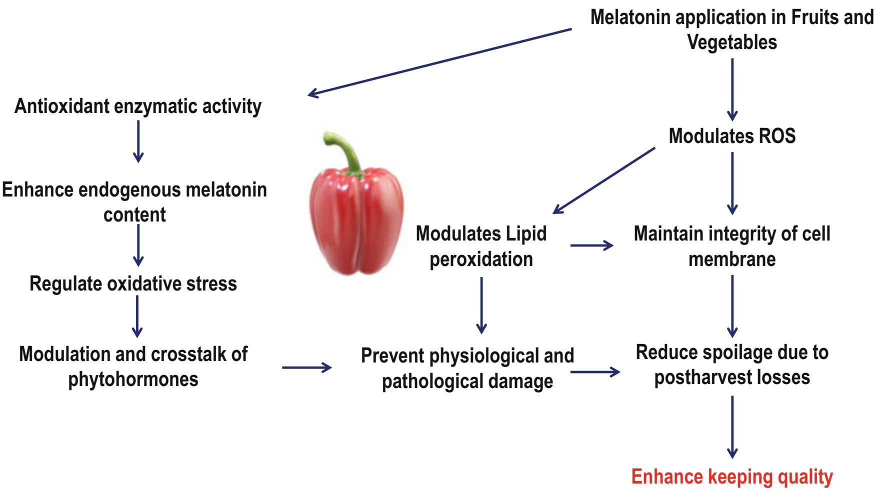

Fig. 10.1 Role of melatonin in post-harvest management of fruits and vegetable

As an exogenously applied substance, melatonin offers promise for extending the shelf life of fruits and vegetables by mitigating post-harvest losses, preserving nutritional quality, and reducing decay during storage. Moreover, the synthesis of endogenous melatonin in fruits and vegetables is explored, shedding light on its natural production and potential implications for post-harvest preservation. Melatonin's exogenous application to fruits and vegetables is primarily the focus of this review. The book chapter also discusses how endogenous melatonin is synthesized, explores how melatonin affects fruits and vegetables after harvest, and explains how it protects perishable items after harvest. Furthermore, the book chapter emphasizes the significance of ROS (reactive oxygen species) signaling throughout these processes (Fig. 10.1).

10.3 Post-harvest Changes in Vegetables and Fruits

According to epidemiological studies (McCann et al. 2005; Tiwari and Cummins 2013), fruit and vegetable consumption is associated with numerous health benefits. These foods are known for their ability to quench free radicals, thereby reducing oxidative damage that can contribute to chronic disease development. Fruits and vegetables have health-promoting properties largely due to phytochemicals, a diverse group of metabolites found in many plants (McCann et al. 2005). Earlier the researchers have extracted phytochemicals from fruits and vegetables to create formulations that offer beneficial effects on the health of humans and animals alike (Jenkins et al. 2008; Leonti et al. 2010). Fruits and vegetables contain a wide variety of phytochemicals, and they are usually classified according to their role, chemical structure, and origin. In different fruits and vegetables, the amount of specific phytochemicals varies significantly depending on the cultivar (Nuutila et al. 2003). The concentration of phytochemicals in these foods is also influenced by factors such as climate, growing location, agronomic practices, and harvest timing, including maturity stage (Nuutila et al. 2003; Raigond et al. 2020; Thakur et al. 2020; Kumar et al. 2020c).

In addition to pre-harvest factors, various post-harvest stages, including food processing, have a significant impact on phytochemical stability in fruits, vegetables, and their processed products. As well as conventional thermal processing, modern or non-thermal methods can degrade phytochemicals in processed foods (e.g., high-pressure processing, pulsed electric fields, ultrasound/sonication, ozone, ultraviolet) (Aaby et al. 2005; Rawson et al. 2010). Even domestic food preparation techniques such as washing, peeling, and cutting can affect phytochemical content. The levels of phytochemicals in processed foods are also influenced by industrial processes like canning and drying. In order to maximize the health benefits derived from fruits, vegetables, and their processed products, it is essential to understand the factors that influence their presence and stability. In order to optimize the nutritional quality of these foods and their potential beneficial effects on human health, pre-harvest and post-harvest practices must be considered (Tiwari and Cummins 2013; Singh et al. 2020; Kumar et al. 2020b; Lal et al. 2021).

Several nutrients are found in fruits and vegetables, including phenolic compounds, ascorbic acid (AsA), carotenoids, and minerals, which provide numerous health benefits for humans, including anti-inflammation, antioxidant, diabetes prevention, cancer prevention, and cardiovascular protection (Cömert et al. 2020; Alegbeleye et al. 2022). Globally, tomatoes, apples, bananas, and papayas are consumed, and their production and demand are increasing rapidly. However, many of these fruits and vegetables are highly vulnerable to rapid softening and over-ripening, which is often accompanied by chlorophyll degradation and pathogen development (Thole et al. 2020; Fan et al. 2022c).

Upon harvesting papayas, their fruit peel turns yellow after the fruit has ripened and softened (Fan et al. 2022c). As a result of an increase in disease incidence, late storage results in a slight decrease in lightness, an increase in chroma, and a gradual decrease in hue angle. Changes in color parameters can influence fruit quality and commodity rates. A similar change in fruit firmness, color parameters, and disease incidence was observed in guavas (Fan et al. 2022b). Fruit decay occurs during storage of cherry tomatoes and litchi fruits as a consequence of weight loss and declining fruit firmness (Kumar et al. 2020a; Tiwari et al. 2020a; Yan et al. 2022; Wang et al. 2022).

Researchers are increasingly interested in low-temperature preservation methods for fruits and vegetables. Cold storage slows down ripening and extends shelf life (Liu et al. 2020a). In the event of prolonged storage at low temperatures, chilling injury can occur, resulting in surface pitting, browning, an inability to ripen properly, water-soaked lesions, and rapid decay (Singh and Pal 2008; Murmu and Mishra 2018). Fruits and vegetables offer numerous health benefits, but their post-harvest preservation poses challenges due to rapid softening, over-ripening, and susceptibility to pathogens. When not handled carefully, low-temperature storage can result in chilling injury. Research and development continue to seek the best balance between preserving nutritional value and maintaining quality when storing them (Li et al. 2023a).

10.4 Melatonin's Regulatory Effects on Post-harvest Management

10.4.1 Antioxidant Properties of Melatonin and Reduction of Oxidative Stress

A reaction between reactive oxygen species (ROS) and proteins can damage them by oxidizing their side chains under environmental stress and senescence. Especially vulnerable are sulfur-containing amino acids like methionine and cysteine to ROS. As a means of repairing oxidized proteins(Baraibar and Friguet 2013), living organisms have developed the methionine sulfoxide reductase (MSR) system. The role of the MSR system and its regulation by melatonin has been explored in the context of fruit and vegetable post-harvest preservation. As Zhang et al. (2017) demonstrated, 400 m melatonin significantly increases the expression of *LcMsrA1, LcMsrA2, LcMsrB1,* and *LcMsrB2* in lychee fruit during storage (Zhang et al. 2017). By enhancing the MSR system, viable protein repair mechanisms can be extended and ROS-induced damage can be prevented. According to Yu et al. (2016), increasing the transcription level of oxidative protein repair genes increases 'Jersey' blueberry heat resistance (Yu et al. 2016).

There are relatively few studies on the enzyme repair system of oxidized proteins in fruits and vegetables despite the importance of the MSR system in post-harvest preservation. The advancements in omics technologies, including transcriptomics, proteomics, and metabolomics, will allow future studies to uncover novel functions for enzymes involved in oxidative protein repair and to better understand how melatonin regulates the MSR system in fruits and vegetables after harvest (Xu et al. 2019b). Protein repair and oxidative damage protection mechanisms can provide valuable insights into improving post-harvest storage conditions and developing effective preservation strategies for fruits and vegetables, resulting in improved quality and longer shelf lives.

A number of hormones have been shown to have significant effects on fruit and vegetable post-harvest preservation, including ethylene (ET), salicylic acid (SA), gibberellins (GAs) such as GA1, GA3, GA4, and GA7, methyl jasmonate (MeJA), and abscisic acid (ABA). There has been increasing evidence suggesting that melatonin plays a key role in maintaining the quality of fruits and vegetables after harvest (Chen et al. 2020; Xia et al. 2021; Fan et al. 2022a). Compared to control groups, exogenous melatonin delayed the decrease in fruit firmness, preserved the hue of fruit peels, and retained greater lightness in papayas during later storage (Fan et al. 2022a). Melatonin alleviates firmness decreases and weight loss in cherry tomatoes (Yan et al. 2022). Furthermore, melatonin treatment results in an evident increase in fruit color indexes (a*/b*) in both sweet cherry and guava fruits (Carrión-

Antolí et al. 2022). The application of exogenous melatonin during the post-harvest period has been shown to inhibit chlorophyll degradation in pepper, broccoli, and Chinese flowering cabbage (Tan et al. 2020). Additionally, melatonin has been shown to reduce decay and disease index in various fruits (Zhang et al. 2021b). In addition, melatonin treatment increases the contents of essential compounds in fruits and vegetables, such as total soluble solids, sugar, protein, ascorbic acid (AsA), carotenoids, flavonoids, and phenols (Fan et al. 2022c; Verde et al. 2022). Furthermore, melatonin has been shown to mediate the production of aroma volatiles, such as propyl acetate and hexyl acetate, in post-harvest pear fruits (Liu et al. 2019; Wei et al. 2022). Together, these studies demonstrate how melatonin enhances the post-harvest preservation of fruits and vegetables in a multifaceted manner. As a result, it has been associated with positive effects on firmness, color, nutrient content, decay resistance, and aroma, making it a potential candidate for improving these perishable commodities' quality and shelf life (Xu et al. 2019a, b; Jayarajan and Sharma 2021; Li et al. 2023a).

Melatonin, also called *N*-acetyl-5-methoxytryptamine, is an endocrine compound that has diverse physiological and cellular functions (Tan et al. 2016). Sleep and circadian rhythms are modulated, immunity is enhanced, and anti-inflammatory effects are observed. It has been shown that melatonin can improve anti-inflammatory activity, particularly in chronic inflammation associated with various diseases (Nabavi et al. 2019; Zhao et al. 2019; Hardeland 2019). The first discovery of melatonin in plants was made in 1995 (Dubbels et al. 1995). Since then, it has been found in several plant species and parts, including rice, wheat, tomatoes, apples, strawberries, grapes, peppers, cucumbers, and solanaceous plants (Altaf et al. 2023a). A key signaling molecule, melatonin is essential for multiple physiological processes in plants, including alleviating abiotic and biotic stresses, regulating plant growth, and regulating development (Gu et al. 2017; Chen et al. 2018; Su et al. 2021). Studies have also shown that melatonin plays a crucial role in fruit and vegetable preservation after harvest (Zheng et al. 2019; Cano et al. 2022). Broccoli, pears, and Zizyphus jujuba fruit have been shown to increase endogenous levels of melatonin when applied exogenously (Zheng et al. 2019). As a result, melatonin effectively reduces reactive oxygen species (ROS) accumulation (Fig. 10.1) by enhancing antioxidant capacity and total phenolics and ascorbic acid (AsA), thereby improving fruit and vegetable quality (Wang et al. 2021). Additionally, melatonin has been shown to enhance polyphenol accumulation and antioxidant capacity in grape berries through ethylene signaling (Xu et al. 2017). It has been demonstrated that melatonin plays a significant and multifaceted role in plant physiology, stress responses, and post-harvest preservation of fruits and vegetables. For agriculture and horticulture, it holds promise for improving crop productivity and quality (Li et al. 2023a).

10.4.2 Melatonin and Signaling

Reactive oxygen species (ROS) encompass a group of molecules, primarily including hydrogen peroxide (H_2O_2), hydroxyl radical (OH), superoxide anion ($O_2^{\bullet-}$), and singlet oxygen ($^1O_2$) (Dietz et al. 2016). These ROS molecules can induce the oxidation of lipids, damage proteins, and alter the structures of various small molecules (Mittler et al. 2022). In response to the potential harm caused by ROS, plants have developed sophisticated antioxidant strategies to regulate ROS homeostasis. These strategies involve both enzymatic and non-enzymatic antioxidants. Enzymatic antioxidants, such as catalase (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD), and glutathione peroxidase (GPX), play essential roles in neutralizing ROS (Gu et al. 2021, 2022). On the other hand, non-enzymatic antioxidants, including glutathione (GSH), ascorbic acid (AsA), flavonoids, carotenoids, and alkaloids, among others, also contribute to ROS scavenging and protection against oxidative damage. Interestingly, studies have revealed that ROS serve dual roles in signaling networks involved in plant stress responses and developmental processes (Mittler 2017). ROS can act as signaling molecules, transmitting information about environmental stresses, and regulating various physiological and developmental responses in plants. Intriguingly, research has suggested that there is a signaling crosstalk between melatonin and ROS in red pear and strawberry fruits during the post-harvest period. This suggests that melatonin may interact with ROS signaling pathways, potentially contributing to the post-harvest preservation of these fruits (Aghdam and Fard 2017; Sun et al. 2021).The delicate balance between ROS production and the antioxidant defense system is crucial for plant survival and adaptation to various environmental conditions. Understanding the interplay between ROS and melatonin signaling may offer new insights into enhancing the post-harvest quality and shelf life of fruits and vegetables through targeted manipulation of these pathways (Caniato et al. 2003; Bal 2019; Tan et al. 2020).

It has been demonstrated that exogenous melatonin significantly improves abiotic stress tolerance as well as heavy metal tolerance in crops, vegetables, and fruits in numerous experiments. Melatonin treatment has been shown to improve cucumber seedlings' tolerance to high temperatures (Zhang et al. 2014) and tomato plants' tolerance to cold stress (Ding et al. 2017) and tea plants' tolerance to cold stress (Li et al. 2018). Moreover, melatonin has been shown to improve salt stress tolerance in rice (Liang et al. 2018) and watermelon, as well as cadmium tolerance in tomatoes (Hasan et al. 2015) and wheat seedlings (Ni et al. 2018). Also, watermelon seedlings were shown to be more resistant to vanadium stress after melatonin treatment (Nawaz et al. 2018). Besides exogenous applications, transgenic approaches have produced melatonin-enriched plants with promising properties. In transgenic Arabidopsis, for example, overexpression of *MzASMT*, *MzSNAT5*, or *TaCOMT* increases the level of melatonin and drought tolerance (Yang et al. 2019; Wang et al. 2019). In both cases, rice plants overexpressing rice serotonin *N*-acetyltransferase 1 and human serotonin *N*-acetyltransferase showed resistance to cadmium as well as cold stress (Kang et al. 2010; Lee and Back 2017). In a similar manner, Arabidopsis plants that were overexpressed with alfalfa SNAT showed a higher tolerance to cadmium than their wild-type counterparts. The overexpression of ovine AANAT and HIOMT genes in switchgrass was found to be effective at increasing growth performance and salt tolerance (Huang et al. 2017). In addition, Xu et al. (2016) found that endogenous melatonin manipulation by overexpressing ASMT enhanced thermotolerance in tomato plants (Xu et al. 2016). Despite the fact that there has been significant research in the field of improving abiotic stress resistance through transgenic approaches, the application of transgenic methods to promote the post-harvest preservation of fruits and vegetables has not been studied to the same extent. Insights gained from enhancing abiotic stress tolerance by using transgenic techniques could provide valuable clues about how to improve fruit and vegetable preservation after harvest (Tiwari et al. 2020b; Jayarajan and Sharma 2021; Altaf et al. 2021a, 2022c; Saqib et al. 2023).

Melatonin has been recognized as a potent free radical scavenger and antioxidant, effectively protecting membrane lipids and proteins against damage caused by free radicals (Reiter et al. 1999). Several studies have reported on the antioxidant capacity of melatonin in various fruits and vegetables, such as peaches (Cao et al. 2016; Gao et al. 2016), cassava, banana, and cucumbers. These findings suggest that melatonin plays a significant role in the post-harvest preservation of fruits and vegetables (Meng et al. 2014; Ye et al. 2016; Su et al. 2019; Wang et al. 2022). Numerous studies have demonstrated that melatonin, similar to plant hormones, exerts crucial regulatory effects on plant processes such as seed germination, growth and development, maturation and senescence, biological rhythm, and stress resistance (Posmyk et al. 2008; Tan et al. 2013; Arnao and Hernández-Ruiz 2014). The multifaceted functions of melatonin in plants offer promising avenues for enhancing the preservation of fruits and vegetables after harvesting. By understanding and harnessing the regulatory capabilities of melatonin, researchers and practitioners can potentially develop novel strategies to extend the shelf life and quality of these perishable agricultural products (Xu et al. 2019a; Li et al. 2023a). As the field continues to advance, the application of melatonin in post-harvest preservation may prove to be a valuable asset in ensuring food security and reducing food waste. There has been extensive research into melatonin's role in crop preservation after harvest in horticulture. In horticultural crops, melatonin appears to delay the aging process and maintain their post-harvest quality, according to existing literature. By scavenging free radicals, protecting cell membrane integrity, regulating fruit ripening and senescence, and enhancing disease resistance, various mechanisms are used to achieve this (Yun et al. 2022).

Melatonin has been shown to promote post-harvest tomato ripening and improve fruit quality by activating gene expression, including the SlACS4 gene in tomatoes, which induces ethylene synthesis (Sun et al. 2015). Horticultural products are affected by melatonin regulation in a variety of physiological and quality ways. For instance, it affects breath intensity after harvest, ethylene release, and antioxidant enzyme activity. Furthermore, it affects the color, bioactive substance content, and antioxidant activity of these crops (Xia et al. 2021). It is believed that melatonin regulates metabolism, gene expression, and protein expression in post-harvest preservation. As a natural and effective tool for prolonging shelf life, maintaining quality, and improving the resistance of horticultural products to post-harvest degradation, melatonin has great promise (Ze et al. 2021). Researchers and practitioners can improve food security and reduce food waste by better understanding the intricate regulatory processes involved in preserving and utilizing horticultural crops (Badria 2002; Mercolini et al. 2012).

10.5 Melatonin's Role in Regulating Enzymatic Activities During Storage

There has been a growing interest in the role hormones play in fruit and vegetable post-harvest performance (Xiang et al. 2020). The shelf life of these produce items is significantly influenced by two key hormones ethylene (ET) and abscisic acid (ABA), which modulate senescence. In order to synthesize ethylene, the enzyme ACC synthase (ACS) converts *S*-adenosylmethionine into 1-aminocyclopropane-1-carboxylate (ACC). Subsequently, the enzyme ACC oxidase (ACO) oxidizes the ACC. This pathway is rate-limiting for both ACS and ACO, so the expression of genes that encode these enzymes can be regulated to reduce ethylene accumulation, thereby delaying fruit and vegetable senescence (Zhang et al. 2022). There is also evidence that the hormone ABA promotes fruit coloration by inducing the accumulation of flavanols and anthocyanins in apples, grapes, tomatoes, and litchis (Villalobos-González et al. 2016). Additionally, hormones such as jasmonic acid (JA) and salicylic acid (SA) have been linked to disease resistance during the post-harvest period (Yin et al. 2023). By expressing JA synthesis genes, MeJA treatment increases the activity of allene oxide cyclase (AOC), which leads to increased endogenous JA production. On the other hand, DIECA treatment reduces endogenous levels of JA, as well as AOC and 12-oxo-phytodienoic acid reductase activities, showing a significant correlation between JA and chlorophyll content in broccoli flowers, a factor contributing to post-harvest yellowing (Fang et al. 2020). In litchis, SA-mediated defense response has been implicated in combating downy blight by modulating fruit senescence (Yin et al. 2023). Also present in very low amounts are auxins, cytokinins (CK), and gibberellins (GAs), which have been associated with anti-senescence activity (Li et al. 2016). By understanding how these hormones play a role in regulating post-harvest processes, we can develop strategies to extend the shelf life of fruits and vegetables and improve their quality.

Melatonin modulates hormone levels significantly during the post-harvest period of fruits and vegetables (Liu et al. 2016), as demonstrated by many studies. By inhibiting the accumulation of ethylene (ET) and abscisic acid (ABA), melatonin has been found to effectively delay senescence in these produce items. As an example, when melatonin is applied externally, ACSs and ACOs genes are inhibited, which reduces ethylene production and delays color changes in bananas and tomatoes (Sun et al. 2020). Melatonin also inhibits ethylene production and respiration rates in pear fruit, which ultimately delays senescence by inhibiting the expression of ET synthetase genes (PcACS and PcACO). Kiwifruit has also been observed to be inhibited by melatonin during storage (Cheng et al. 2022). Furthermore, melatonin has been shown to inhibit the expression of ET transcription factors (*AdERF4*, *AdERF74*, and *AdERF75*) in kiwifruit and to suppress ET release. Moreover, melatonin has been shown to reduce ABA levels in Chinese flowering cabbage by modulating ABA synthesis and chlorophyll degradation by repressing *BrABF1*, *BrABF4*, and *BrABI5* (Tan et al. 2019). Post-harvest disease resistance in fruits has been linked to melatonin. Melatonin induces the expression of jasmonic acid synthesis genes in blueberries, which leads to increased JA accumulation and modulation of jasmonic acid signaling pathways, improving disease resistance. Additionally, exogenous application of melatonin inhibits gray mold development caused by B. cinerea in tomatoes by increasing chitinase and 1,3-glucanase activity (Li et al. 2019a). During post-harvest decay in Angeleno plums, melatonin appears to increase gibberellins (GAs), specifically GA1. Auxin and ethylene signaling pathways, as well as redox homeostasis in banana fruit peels, are all involved in which melatonin interacts with various transcription factors like WRKY, MYB, ERF, ARF, and bHLH3 (Zhang et al. 2021a; Cheng et al. 2022). Melatonin regulates the release of hormones like ET, ABA, SA, and others, thereby extending the shelf life of fruits and vegetables. To fully understand the molecular mechanisms underlying the effects of melatonin on fruit and vegetable preservation and disease resistance during storage, more genetic research is needed (Li et al. 2019b; Zhang et al. 2021a; Aghdam et al. 2023).

Melatonin's biosynthesis and catabolism in plant responses to abiotic stresses was extensively covered in our previous reviews (Su et al. 2021). Plants accumulate melatonin as a result of various abiotic stresses, including salinity, heat, cold, drought, and exposure to cadmium. Melatonin content has increased largely because genes encoding enzymes involved in its biosynthesis have been upregulated, including tryptamine 5-hydroxylase (T5H), tryptophan decarboxylase (TDC), *N*-acetylserotonin methyltransferase (ASMT), serotonin *N*-acetyltransferase (SNAT), and caffeic acid *O*-methyltransferase (COMT) (Cano et al. 2022). The endogenous melatonin content of cherry fruit increased from 0 to 14 days during storage (Bhardwaj et al. 2022), but then decreased from 14 to 63 days. A similar pattern was observed for melatonin content in table grapes, mangoes, cassava, and strawberries during the post-harvest period (Arabia et al. 2022). Melatonin accumulation, however, showed an opposite trend in "Summer black" grapes. Additionally, melatonin levels decreased during the post-harvest period in angeleno plums, pakchoi, and cherry tomatoes (Liu et al. 2020b). It is important to note that factors such as growth stage, harvesting time, and storage conditions influence melatonin accumulation during the post-harvest period. In cherry fruit, for example, endogenous melatonin accumulation was affected not only by storage period but also by growth period, as it decreased significantly from anthesis to maturity (Xia et al. 2020). The expression patterns of genes involved in melatonin biosynthesis, including TDCs, T5Hs, SNATs, and ASMTs, were also found to be differentially regulated in various fruits and vegetables following harvest (Liu et al. 2020b). Melatonin metabolism in different post-harvest contexts is complex due to these dynamic and highly regulated changes in melatonin accumulation and gene expression. The accumulation of melatonin in fruits and vegetables during the post-harvest period is influenced by various factors and follows a different pattern depending on the specific crop. By understanding the regulation of melatonin biosynthesis and its changes during post-harvest storage, we can improve the quality and shelf life of agricultural products.

10.6 Conclusion

This chapter highlights the widespread presence of melatonin in fruits and vegetables and explores its changes in content and synthesis sites during the post-harvest period. Fruits and vegetables have been found to have several beneficial effects when exogenous melatonin is applied following harvest. As a result of exogenous melatonin, endogenous melatonin accumulates, which can lead to a variety of beneficial effects. In addition to improving fruit and vegetable quality, it reduces weight loss, reduces fruit firmness decline, and prevents discoloration. As a result, these perishable products are more likely to be preserved because decay and disease are reduced. In addition, exogenous melatonin supplementation increases the amount of bioactive compounds in fruits and vegetables. In addition, it increases glutathione (GSH), ascorbic acid (AsA), dehydroascorbic acid (DHA), anthocyanins, carotenoids, flavonoids, and phenols, which are important antioxidants. At the same time, it decreases the content of harmful substances such as malondialdehyde (MDA), hydrogen peroxide (H_2O_2), and superoxide radicals ($O_2^{\bullet}$). As a result, the antioxidant capacity of the treated fruits and vegetables is significantly improved.

Several antioxidant enzymes are also enhanced by exogenous melatonin, including catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), glutathione peroxidase (GPX), dehydroascorbate reductase (DHAR), and monodehydroascorbate reductase (MDHAR). In addition to improving antioxidant defense system, this boost in enzyme activity also protects fruits and vegetables from oxidative stress post-harvest. Melatonin also increases proline content and decreases membrane lipid peroxidation, thereby preserving the integrity of cell membranes in fruits and vegetables during cold storage. In addition, exogenous melatonin regulates plant hormones, including ethylene, salicylic acid, and abscisic acid, among others. As a result of this regulation, fruits and vegetables are protected against bacterial invasion and delayed post-harvest senescence.

In order to achieve optimal shelf life extension and quality preservation, it is necessary to note that the effective concentrations of melatonin vary by fruit and vegetable species. Therefore, it is crucial to determine the appropriate melatonin concentrations for each type of produce. The application of exogenous melatonin in post-harvest preservation offers numerous advantages, including enhancing antioxidant capacity, preserving quality, delaying senescence, and protecting against microbial threats. Fruit and vegetable preservation specialists can reduce food waste and ensure consumers have a steady supply of fresh and high-quality produce by understanding and fine-tuning the application of melatonin. Melatonin was believed for a long time to be an exclusive hormone found only in animals. As a consequence, research on melatonin in plants commenced relatively late, and its role and application in preserving horticultural products such as vegetables, fruits, and cut flowers have only recently gained attention, resulting in relatively few research reports on the subject. Our understanding of melatonin's role and mechanism in plants has improved significantly as research on the plant field has intensified. Melatonin has therefore become increasingly important for ensuring the quality of horticultural products and has potential applications that are being explored.

Melatonin has been found to have numerous physiological effects in plants, including scavenging free radicals within cells, maintaining cell membrane integrity, regulating fruit ripening, delaying leaf senescence, and enhancing plant resistance. A number of scholars have also conducted in-depth investigations to determine how melatonin preserves certain horticultural products physiologically, biochemically, and molecularly. There are, however, still certain aspects associated with melatonin in horticulture that require further research and attention despite these advances. A further exploration and strengthening of research efforts is required for melatonin's effect on fruit ripening and aging, its application in cut flower preservation, and its potential for improving post-harvest stress resistance in horticultural products.

Furthermore, it is important to examine melatonin in combination with other preservatives. Current research focuses primarily on melatonin's effect on post-harvest preservation by itself. In addition to salicylic acid and NO, other plant signaling molecules have also been shown to improve horticultural crop quality and aging. In order to understand the mechanism of action for preservation, it is critical to understand how these signaling molecules interact with melatonin and potentially counteract its effects. Several abiotic factors, including mechanical damage, temperature, humidity, light, and gas composition, significantly affect the storage, transportation, and circulation of horticultural crops after harvest. Melatonin regulation may also be affected by these factors. As a result, future research must take into account the actual conditions of post-harvest storage and transportation, incorporating the needs of production companies to study the coordination and mutual support of melatonin and other factors in regulating horticultural crop preservation after harvest. By increasing antioxidant enzyme activity as well as non-enzymatic antioxidants, melatonin plays an important role in preserving post-harvest fruits and vegetables by scavenging reactive oxygen species (ROS). It also regulates genes related to oxidative protein repair, maintains cellular redox homeostasis, and eliminates excess ROS as an antioxidant. This provides a promising foundation for future research aimed at prolonging the shelf life of fruits and vegetables with the application of exogenous melatonin. The shelf life of fruits and vegetables could be extended by increasing endogenous melatonin levels by using a transgenic approach to further enhance preservation. It may be beneficial to identify genes involved in melatonin biosynthesis in fruits and vegetables and engineer crops with a higher melatonin content. Despite progress in understanding melatonin's function in post-harvest preservation, more research is needed to fully understand its mechanisms. For practical application in post-harvest fruit and vegetable storage, it is necessary to evaluate how melatonin and classical preservation technologies work together.

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

11

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Abstract

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

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

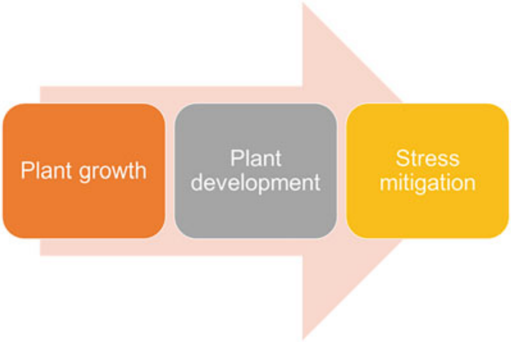
Keywords

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

11.1 Introduction

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

Fig. 11.1 Major role of melatonin in plants



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

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

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

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

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

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

11.2 Melatonin: Provoking Defense Mechanisms against Various Stresses in Plants

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

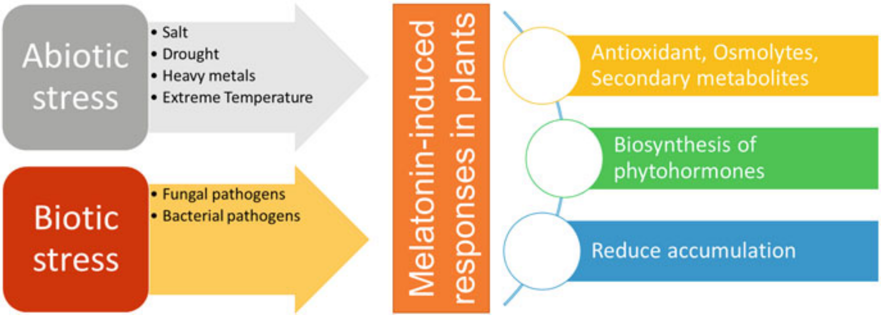


Fig. 11.2 Melatonin provokes defense against multiple stresses in plants

11.2.1 Melatonin Against Abiotic Stressors

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

11.2.2 Melatonin Application Alleviates Drought Stress

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

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

11.2.3 Melatonin and Salt Stress

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

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

11.2.4 Melatonin Treatment under Temperature Fluctuations

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

11.2.5 Melatonin and Heavy Metal Toxicity

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

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

11.3 Melatonin against Biotic Stressors

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

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

11.4 Melatonin: A Multifunctional Factor in Plants

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

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

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

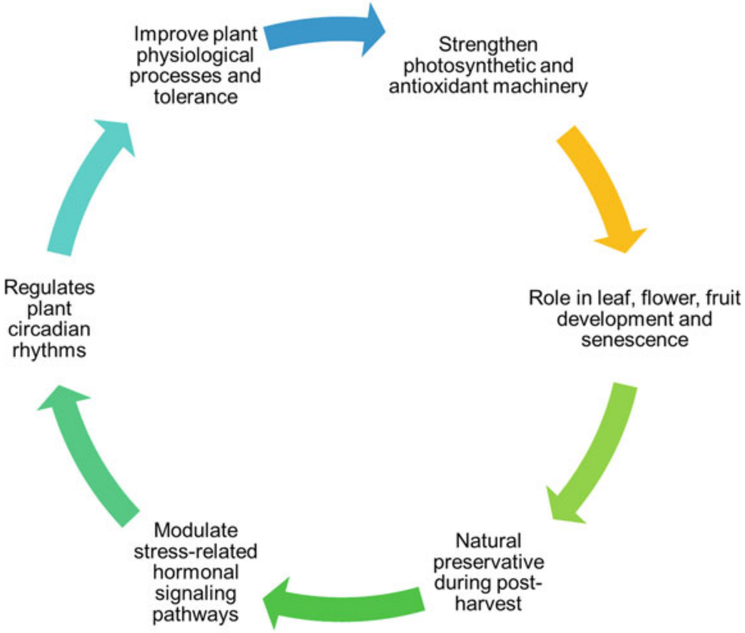


Fig. 11.3 Multifunctional role of melatonin in plant growth, development, and stress tolerance

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

11.5 Synergistic Response of Melatonin Biosynthesis with Other Hormones

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

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

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

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

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

11.6 Regulation of Melatonin-Mediated Plant Growth and Development

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

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

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

11.7 Conclusion and Future Perspectives

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

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

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Melatonin-Mediated Regulation of Growth, Production, and Protection in Forest Plant Species

12

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Abstract

Melatonin (N-acetyl-5-methoxytryptamine), a pleiotropic signalling molecule with plethora of physiological and cellular functions, previously known to occur in animals, was discovered in plants in 1995. Plant melatonin, also referred to as phytomelatonin, has shown to be ubiquitously produced in plants. It has a variety of effects in plants, including its protective role against a wide range of biotic and abiotic stressors, stimulating growth and development especially rhizogenesis, increasing secondary metabolite production, and mediating various other physiological processes such as seed germination, flowering and fruit ripening, circadian rhythms and photoperiodic traits, photosynthesis, osmotic regulation, hormone levels and signalling, and gene expression. As a number of biotic and abiotic stressors greatly limit the growth and development of forest plants and restrict the regeneration and afforestation, understanding the role of melatonin in forest plant species may help in developing practical applications to combat these issues. Since the melatonin's discovery in plants, several studies have provided the understanding of its role in agricultural and horticultural crops; though melatonin has been discovered in a number of forest plant species, detailed research has been carried out for relatively few species, which limits our understanding of the role it plays in forestry. In this chapter, we discuss the occurrence of melatonin, its role in modulation of growth and development, and protection against various stressors in forest plant species.

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Keywords

Phytomelatonin · Stress tolerance · Physiology · Forests

12.1 Introduction

Forests play fundamental role in sustaining life on earth. They are key regulators of climate, biodiversity conservation, water cycling, soil conservation, and overall global well-being. They also provide a wide range of economic benefits, such as timber and nontimber forest products (NTFP). Forest cover represents nearly 4.06 billion hectares (31%) of the earth's land surface. Forest cover has decreased by approximately 420 million hectares due to deforestation worldwide since 1990 (FAO 2020). The total area of the world's forests is still anticipated to continue to decline even though the annual pace of forest loss has slowed down (Keenan et al. 2015). The biotic and abiotic stresses cause significant losses in forestry by slowing growth and development (Mandal et al. 2022; Mangal et al. 2022). In 2015, these stresses caused severe damage to approximately 40 million hectares of forests, mostly the temperate and boreal forests (FAO 2020). Forests are becoming more vulnerable to various stresses due to changing climate conditions, and global movement of insect-pests and pathogens (Teshome et al. 2020). Despite the lack of thorough evaluations of losses, there are sufficient evidences to suggest that these stresses have significant impact on the forestry sector (Schuldt et al. 2020). These stress factors significantly affected 141.1 million hectare of forest cover in 75 countries from 2003 to 2012 (FAO 2015). Furthermore, these inimical factors drastically affect the ecological services of forests (Keenan et al. 2015).

Melatonin (N-acetyl-5-methoxytryptamine) is a ubiquitous molecule found in all kingdoms from bacteria to animals (Mannino et al. 2021; Rehman et al. 2022; Zhao et al. 2019). Melatonin, first isolated in bovine pineal gland (Lerner et al. 1958), was discovered in plants after almost four decades (Hattori et al. 1995; Dubbels et al. 1995). Murch et al. (2000) confirmed its synthesis in *Hypericum perforatum* (L.) by an isotope tracer study. Melatonin, also referred to as phytomelatonin in plants, is a pleiotropic signalling molecule exhibiting variety of functions including protection against abiotic and biotic stressors, plant growth regulation, gene expression modulation, etc. (Arnao and Hernández-Ruiz 2015; Agathokleous et al. 2021; Sun et al. 2021; Murch and Erland 2021; Altaf et al. 2022b, c, d). In addition to its function as a signalling molecule and ability to upregulate a number of antioxidant enzymes, melatonin also acts as a scavenger of many free radicals, reactive oxygen species (ROS), and reactive nitrogen species (RNS) (Debnath et al. 2019). Recent studies revealed that melatonin also regulates the expression of several enzymes, and transcription factors concerned with signalling pathways, including auxin (IAA), gibberellic acid (GA), ethylene (ET), salicylic acid (SA), and abscisic acid (ABA) (Sun et al. 2021; Behera et al. 2022). Furthermore, it is currently understood that melatonin is also involved in the signalling pathways of newer molecules such as nitric acid (NO), strigolactones, and brassinosteroids (Tiwari et al. 2022a, b).

Melatonin also plays a critical role in the rhizosphere interaction between roots and soil microbes, influencing plant growth, ion transport, and nutrient allocation (Asif et al. 2019; Ye et al. 2022). Plenty of research work has been done on the application of exogenous melatonin to alleviate various stresses and to improve growth and productivity (Tiwari et al. 2020; Nawaz et al. 2020). Majority of research on the effects of melatonin on plant growth and stress alleviation has concentrated on agricultural and horticultural crops, with only a few studies focusing on forest plants.

12.2 Melatonin in Forest Plant Species

Several plants produce significant amounts of melatonin. Despite the fact that melatonin appears to be present in all plants, little is known about its presence in forest plant species. Chen et al. (2003) investigated 108 herbs for the presence of melatonin and observed that all the herbs contained melatonin ranging from 12 to 3771 nanogram per gram of the plant tissue. Zohar et al. (2011) recorded significant levels of melatonin in the leaves and fruits of 31 wild plant species. The melatonin content in different plant forms (climbers, shrubs and trees) was found to vary significantly, with trees having the highest levels. Melatonin levels exhibit positive correlation in the leaves and fruits of various species. Nonetheless, melatonin levels in fruits were often lower than those in leaves. In *Cannabis sativa*, melatonin concentration in seeds varied from 13.43 to 30.40 ng g^{-1}, while in the aerial parts it varied between 1.16 and 4.85 ng/g (Allegrone et al. 2019). Some studies have been carried out on the impact of melatonin on forest plants, and the findings suggest that melatonin can have a positive impact on plant growth and stress tolerance.

12.3 Melatonin as Plant Growth Regulator

Melatonin is a signalling molecule that plays critical role in regulation of various processes concerned with plant growth and development. Like indole acetic acid (IAA), melatonin functions as a growth regulator within plant body (Hasan et al. 2015). It performs an array of physiological functions (Fig. 12.1) such as circadian rhythm modulation, increasing seed germination, growth, and enhancement of resistance to stresses (Rodriguez et al. 2004; Xu et al. 2013; Zhang et al. 2014). Several studies suggest that the melatonin has meticulous physiological functions in plants, including promoting primary root growth, adjusting the branching and growth patterns of aerial parts, inhibiting leaf senescence by enhancing photosynthesis, accumulation of biomass, and stimulating caulogenesis and rhizogenesis in various species (Zhang et al. 2012; Chourasia et al. 2022). It also stimulates physiological activities like photosynthesis, stomatic absorption, osmoregulation, primary and secondary metabolism, as well as the regulation of plant hormones (Arnao and Hernández-Ruiz 2018). Melatonin regulates photoperiod and circadian rhythms in plants by controlling the link between the light harvesting complex and antenna complex of photosystem II (PS II), which aids in the repair of the

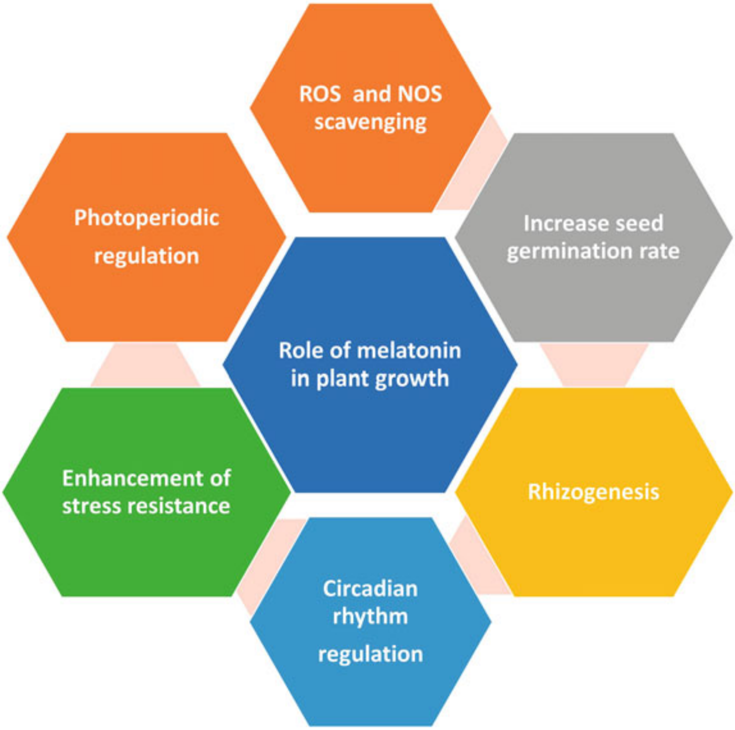

Fig. 12.1 Role of melatonin in plant growth. *ROS* reactive oxygen species, *NOS* nitric oxide synthase

photosynthetic apparatus, prevention of chlorophyll degradation during senescence of leaves (Shi et al. 2015b).

Melatonin as a chronoregulator served as the impetus for its study in plants; more particularly its possible involvement in circadian rhythms regulation and photoperiodicity. According to Kolář et al. (2003) melatonin was found in 15 days old planted seedlings of *Chenopodium rubrum* and observed the melatonin levels fluctuate in response to the 12:12-h light/dark cycle. Melatonin levels were undetectable during the day but significantly increased during the night (peaking at 250 pg/g FW). Chloroplastic ATP synthases, Rubisco small subunits, Rubisco-interacting protein, and subunit of the photosystem I reaction centre were mainly elevated by melatonin, which is correlated with increased photosynthetic activity. Moreover, melatonin reduced the expression of pheophorbide a oxygenase (PaO), dehydrins, heat-shock proteins, a-glucans, a-glucano-transferase, and senescence dehydration-associated protein. All of these are related with the breakdown of starch granules, which are responsible for decrease in photosynthetic activity and prominent starch degradation during leaf senescence, a process that is slowed down by melatonin. Melatonin inhibits the expressions of proteins involved in protein folding and post-translational modifications, including certain serine/threonine protein kinases/phosphatases and mitogen-activated protein kinase (MAPK) (Wang et al. 2014). It removes ROS and RNS, such as O^{2-}, OH^-, NO, and peroxynitrite (ONOO) and works to enhance the redox state. In addition to inducing the production of numerous vital enzymes necessary for detoxifying too much H_2O_2 during this regulation process are catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), AsR/GR, and peroxiredoxin (Prx) (Sharif et al. 2018).

Fazal et al. (2018) evaluated the effects of exogenous melatonin application on *Prunella vulgaris*, an important medicinal herb. Growth characteristics and stress enzyme production were evaluated and results revealed that applying melatonin exogenously at 0.5 and 1.0 mg/L concentration increased the biomass production. Melatonin at concentration 1.0 mg/L stimulated the production of total protein and protease activity in callus cultures. It also boosted the activity of superoxide dismutase and peroxidase enzymes in leaf-derived callus cultures. The naphthalene acetic acid (NAA) and melatonin synergistically increased growth, total protein level and activity of protease in leaf and petiole derived cultures. In other study on *P. vulgaris* exogenous application of melatonin at concentrations of 50–200 μM had a positive impact. The treatment at 100 μM resulted in significant improvements in several aspects, including increased levels of superoxide dismutase, peroxidase, soluble sugar, and proline while decreasing malondialdehyde (MDA), hydrogen peroxide (H_2O_2), and relative electrical conductivity. Additionally, it promoted growth, increased photosynthetic pigment content, and improved the performance and coordination of PSI and PSII. The treatment also enhanced the photosynthetic capacity of *P. vulgaris*, increased dry mass, and the accumulation of various phenolics and flavonoids (Chang et al. 2023). During the storage of *Phyllostachys edulis* at 4 °C, melatonin treatment effectively slowed down the lignification process, reducing the rate of yellowing and hardening, as well as reducing the contents of lignin and cellulose. Melatonin treatment also increased antioxidant enzyme activity and decreased the activity of enzymes related to lignin synthesis. Additionally, melatonin inhibited the expression of certain transcription factors related to lignification, suggesting that it may be involved in the regulation of processes associated with lignification of bamboo shoots (Li et al. 2019b). In *Santalum album* seedlings exposed to low or high nitrogen conditions, application of exogenous melatonin increased NH_4^+ and NO_3^- uptake, and nitrate reductase and glutamine synthase enzyme activities. Melatonin also enhanced haustorium development and accelerated nitrogen metabolism via auxin accumulation. Melatonin upregulated genes involved in nitrogen metabolism and auxin signalling pathways (Meng et al. 2021). Abbas et al. (2021) investigated the effects of melatonin on the emission of volatile organic compounds in *H. coronarium* flowers at different stages of development. Results revealed that melatonin treatment significantly increased the volatile compounds emission, with the highest emission occurring during the full bloom stage. Transcriptome sequencing identified differentially expressed genes, and certain volatile organic compounds were found to be linked with these genes. Additionally, some transcription factors were also upregulated. In *Pinus nigra*, exogenous melatonin application resulted in improved seedling characteristics, viz. growth, chlorophyll content, and glucose and sucrose content. The results showed that low

Table 12.1 Role of melatonin in growth and development of forest plant species under non-stress conditions

Plant name	Melatonin dose	Response	References
Phyllostachys edulis	1 mM	Slowed lignification of shoots; inhibited the phenylalanine ammonia-lyase and peroxidise activity; increased the antioxidant enzymes activity	Li et al. (2019b)
Santalum album	1 μM	Improved growth by enhancing nitrogen metabolism and haustorium formation; increased NO_3^- uptake under high nitrogen and NH_4^+ uptake under low nitrogen	Meng et al. (2021)
Pinus nigra	250, 500, 1000, 1500 μM	High doses of melatonin decreased the levels of certain macro- and micro-elements	Celik (2021a, b)
Hedychium coronarium	50, 100, 500, 1000 μM	Increased floral scent production by modifying gene expression in the volatile organic compound biosynthesis pathway	Abbas et al. (2021)
Prunella vulgaris	0.5, 1.0 mg/L	Increased biomass accumulation, total protein content, and enhanced antioxidant activity	Fazal et al. (2018)
	50, 100, 200, 400 μM	Increased antioxidant activity, decreased malondialdehyde and hydrogen peroxide, increased photosynthetic content	Chang et al. (2023)
Perilla frutescens	25, 50, 100, 150, 200 μM	Enhanced antioxidant enzymes activity, chlorophyll concentrations; increased root and shoot biomass in dose-dependent mode	Xiang et al. (2019)
Chenopodium rubrum	100, 500 μM	Modified flowering time with calcium/calmodulin signalling	Kolář et al. (2003)
Stevia rebaudiana	5, 20, 100, 500 μM	Dose dependent improved seed germination, increased biomass, upregulated genes	Simlat et al. (2020)
		Lower concentrations improved germination while high concentration inhibited it; increased catalase and peroxidise activities	Simlat et al. (2018)

doses (250–500 μM) of melatonin had the most significant impact on both morphological and biochemical variables. Melatonin enhanced seedlings' resistance to low temperatures and semi-arid climates by supporting metabolic processes and increasing antioxidant enzyme activity (Çelik et al. 2023). Some forest plant species and role of melatonin in their growth and development are listed in Table 12.1.

12.4 Melatonin-Mediated Alleviation of Biotic and Abiotic Stresses in Forest Plants

The unsuitable circumstances that impede the daily life processes of plants are known as 'stress'. Like other crops, forest plants are inevitably affected by a variety of unfavourable conditions that restrict their ability to flourish in the environments

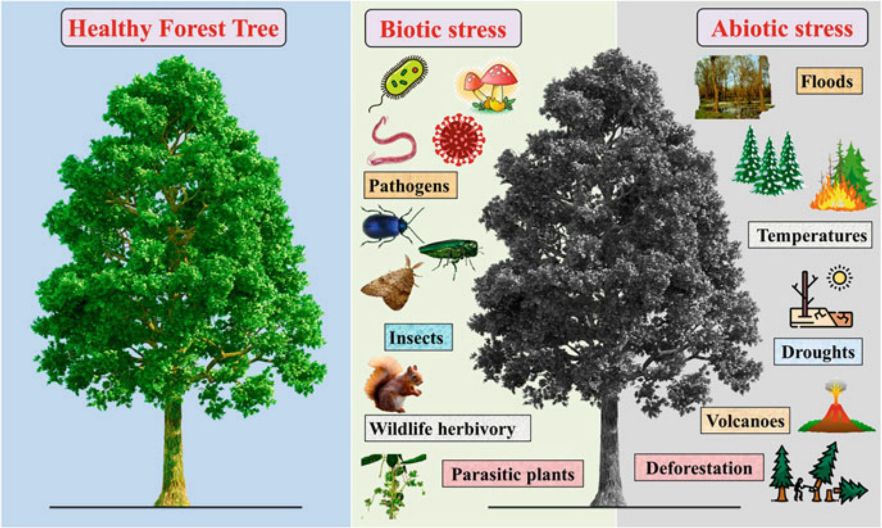

Fig. 12.2 Biotic and abiotic stresses affecting plant growth and development

where they are grown (Devi et al. 2022a, b). Stressors that have a detrimental effect on forest plants are basically categorised into two groups: biotic stresses and abiotic stresses (Teshome et al. 2020). Biotic stresses are typically caused by living organisms such as fungi, bacteria, viruses, nematodes, insects, and parasitic plants, whereas abiotic stresses are caused by noxious environmental conditions such as salinity, drought, low and high temperatures, water-logging, and heavy metal contamination (Fig. 12.2). All these stress factors have toxic influences on forest ecosystems and cause economic losses in terms of yield and quality in the forestry sector (Kumar et al. 2022a, b). Forest plant species, during their whole lives, are challenged with catastrophic diseases and herbivorous insects. Forest plant diseases are generally caused by pathogenic microbes, and among microbe-induced diseases, fungi are major threats to forest regeneration and also cause huge mortality in nurseries (Tapwal et al. 2011; Kumar et al. 2021). Leaf spot and wilt are some important diseases that are considered serious problems for forest sector. According to Sommerfeld et al. (2018), temperate forests are invaded severally by variety of insect-pests and diseases (Lal et al. 2021; Tiwari et al. 2021a, b). Among the abiotic pressures, drought and high temperatures (fire) are the most damaging and catastrophic threats for the forest sector. Exposure to stresses leads to accumulation of ROS and NOS that disrupt redox homeostasis, causing macromolecules damage and oxidative stress, and ultimately plant cell death, thereby negatively affecting plant growth (Xie et al. 2019; Chaki et al. 2020).

Interestingly, different strategies have been used to alleviate the harmful impact of biotic and abiotic pressures on forest plants, including cultivars that can withstand stressors, the application of synthetic agrochemicals, resource management approaches, and many other practises that have all been studied worldwide as potential solutions. Moreover, the huge use of agrochemicals in surrounding agriculture and horticulture systems also have toxic effect on forest ecosystems and living organisms present in the forest environment (Rahman et al. 2009; Agathokleous et al. 2022). Nevertheless, these approaches are costly, consume more time, stressful, and may result in the loss of the desired feature in the host gene pool. Nowadays, research is directed at finding environment friendly alternatives to alleviating the dreadful consequences of various stressors. To meet all these demands, one of the most promising approaches is the application of melatonin without causing any harmful effect on the forest environment's sustainability. Melatonin is an environmentally friendly molecule that is synthesised in plants via the tryptophan route and that protects plants from threats and promotes plant growth and development. In recent years, extensive work has been conducted on the application of melatonin to impede adverse stresses in various agricultural crops (Jahan et al. 2021; Altaf et al. 2022a). The limited research in the field of forestry for growth, development, and combating stresses limits our understanding of the role it plays or might play in maintaining the overall health of forest ecosystems.

12.4.1 Melatonin as an Alleviating Candidate against Biotic Stress

Melatonin performs critical roles in the induction of well-equipped biotic stress resistance in plants. Various deformities are induced in plants by stresses such as damage to the membrane system, disturbance of the hormonal balance system, decreased photosynthetic rates, adverse effects on plant respiratory mechanisms, and disturbance of ROS and RNS mechanisms. In plant cells, ROS and RNS generally serve as secondary messengers to maintain redox equilibrium when their concentration is low; however, at high concentration they are poisonous and detrimental to the plant cells due to their strong oxidative capacity (Kapoor et al. 2019; Khan et al. 2023). Melatonin first enhances the ROS and RNS production for starting programmed cell death (PCD) to stop the spread of pathogens under biotic stress situations (Tiwari et al. 2021a, b). Melatonin may encourage plants to improve resistance to diseases by acting as a natural antioxidant and antimicrobial substance to maintain the hydrogen peroxide (H_2O_2) concentration, thickening of the cell wall, improve the antioxidant enzymes activity, and promote photosynthesis, as well as acting as a signalling molecule to modulate the activity of defence-related genes and the signalling pathway of phytohormones, such as salicylic acid (SA) (Liu et al. 2019; Jafari et al. 2022). Melatonin-treated plants exhibit pathogen resistance due to the formation of a thick cell wall as a result of callose, cellulose, and xylose accumulation (Zhao et al. 2015; Moustafa-Farag et al. 2019). Furthermore, this molecule has antimicrobial properties that inhibit the proliferation of microbes and the germination of fungal spores (Kong et al. 2021). Melatonin's role in inducing biotic stress resistance has recently been demonstrated using gene expression analysis (Shi et al. 2015a). Exogenous application of melatonin to plants contributes significantly to disease tolerance by enhancing pathogenesis-related (PR) genes including *PR1*, *PR5*, *PDF1.2*, and *NPR1* and inducing the accumulation of pathogen resistance proteins (TIR-NBS class, MAPKs) (Zhao et al. 2021).

In the field of forestry, studies have been conducted on the role of melatonin in the induction of disease resistance. In American elm (*Ulmus americana*), spike of about 7000 fold was observed in melatonin and serotonin levels after the saplings were subjected to beetle (*Scolytus multistriatus*) feeding, indicating melatonin's role as a signalling molecule mediating reactions to injury caused by insect (Saremba et al. 2017). Yang et al. (2021b) conducted a field experiment to investigate the effect of melatonin on the disease resistance of the forest medicinal herb *Panax notoginseng*. Results revealed that exogenous melatonin application significantly increased phytomelatonin accumulation by increasing the expression of genes involved in its synthesis. Furthermore, 10 μM melatonin applications reduced the incidence of leaf diseases (black spot, round spot, and grey mould) in *P. notoginseng* by upregulating immunity and defence-related genes. These results proposed that dose-dependent foliar application of melatonin could be a potential approach for enhancement of leaf disease resistance in the medicinal herb *P. notoginseng*.

In terrestrial plants, natural openings like stomata can also serve as entry sites for plant pathogens. To minimise the invasion of pathogens after pattern recognition receptors (PRRs), PRRs detect PAMP/MAMPs, plants have a well-developed mechanism to close the stomata, known as stomatal defence or stomatal immunity (Melotto et al. 2017). Flagellin Sensing 2 (FLS2) interacts with its co-receptor Brassinosteroid insensitive 1-associated kinase 1 (BAK1) upon detecting MAMPs (such as bacterial flagellins or flg22), which phosphorylates the heterotrimeric GTP-binding protein Gα subunit (GPA1), which triggers a ROS burst and stomatal immunity via controlling the connection between GPA1 and NADPH oxidase RbohD (Xue et al. 2020). When activated, the MAPK cascades also regulate the metabolism of organic acids, which is crucial for stomatal immunity (Su et al. 2017). It was found that application of melatonin significantly enhanced the innate immunity via NADPH oxidase-mediated ROS and mitogen-activated protein kinase (MAPK)-mediated stomatal defence in *P. notoginseng* against *Pseudomonas syringe* invasion (Yang et al. 2021a).

12.4.2 Melatonin-Mediated Alleviation of Abiotic Stresses

The growth and productivity of plants are significantly affected by abiotic stresses such as salinity, extreme temperatures, drought, heavy metal toxicity, and UV exposure. It has been estimated that around 90% of arable land is susceptible to at least one of these stressors (Khan et al. 2020). In plants, melatonin enhances the stress tolerance either by scavenging reactive oxygen species directly or by improving antioxidant enzymes activity, photosynthetic efficiency, and metabolites content (Khan et al. 2020). In plants, oxidative stress occurs when there is an imbalance between the production of ROS and RNS, and the plant's ability to detoxify them. Melatonin can help to alleviate oxidative stress in plants by several mechanisms,

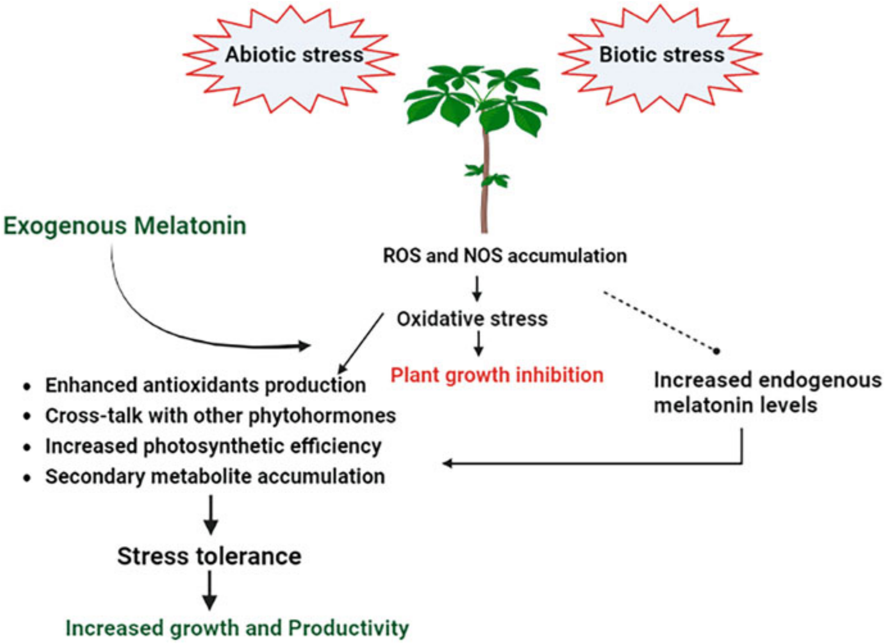

Fig. 12.3 Role of melatonin in biotic and abiotic stress alleviation. *ROS* reactive oxygen species, *NOS* nitric oxide synthase

including scavenging ROS, regulating gene expression, and enhancing photosynthetic efficiency (Arnao and Hernández-Ruiz 2014).

Poplar has been established as a model organism in forestry. It is also known as the *Arabidopsis* of forestry (Taylor 2002). In poplar (*Populus alba* × *Populus glandulosa*) exogenous melatonin significantly lowered lipid oxidation and membrane damage induced by methyl viologen (MV) as demonstrated by decreased relative malonaldehyde content and leakage of electrolyte (Fig. 12.3). Exogenous melatonin application also stimulated activity of antioxidant enzymes, viz. ascorbate peroxidase (APX), superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) (Ding et al. 2018).

12.4.2.1 Salt Stress

Salinity is a major abiotic stressor that restricts the plant growth and productivity. In plants, excessive salt induces water deficit and causes physiological damages by disturbing key biochemical process, viz. photosynthesis, ion homeostasis, and membrane peroxidation (Ryu and Cho 2015; Hao et al. 2021). Salinity stress reduces the acquisition of potassium and calcium ions, increases the adsorption of sodium and chloride ions, and causes an excessive generation of ROS, ultimately resulting in ion toxicity, osmotic stress, and oxidative stress (Yang and Guo 2018).

Numerous previous studies have demonstrated the impact of increased melatonin level in plants under salt stress and use of exogenous melatonin in combating the stress (Li et al. 2019a; Zhan et al. 2019). Melatonin's effects on plants are dose-dependent; it may relieve or aggravate stress in different concentrations (Li et al. 2017). In *Betula platyphylla* seeds exogenous melatonin negatively affected the germination, intensifying the effect of salt stress (Li et al. 2017). Song et al. (2022) found that melatonin acted in dose-dependent way in the alleviation of saline-alkali stress in *Populus cathayana* × *canadensis* 'Xin Lin 1'. Low doses of melatonin (50 μM, 100 μM) had a significant effect in reducing MDA levels in leaves and increasing the activities of antioxidant enzymes (SOD, CAT). Vafadar et al. (2020a) elucidated the role of Melatonin-Ca^{2+} crosstalk and revealed that melatonin and Ca^{2+} triggered systemic tolerance in *Dracocephalum kotschyi*, as it increased relative water and proline level and modulated Na^+, K^+, and Ca^{2+} homeostasis. Root pre-treatment with 100 μM melatonin recovered plant growth enhanced the antioxidant enzyme activity, improved membrane integrity, and reduced leaf electrolytic leakage, ROS, and MDA contents indicating systemic tolerance. Salinity stress raised the endogenous melatonin level and induced Ca^{2+} in *D. kotschyi* leaves. The related study by Vafadar et al. (2020b) revealed that melatonin and Ca^{2+} have a role in the production of specialised metabolites and defence responses against salt stress. Melatonin and Ca^{2+} increased the accumulation of phenolic compounds, viz. luteolin, rosmarinic acid, and apigenin under controlled and stressed conditions and alleviated salt-induced oxidative stress and improved antioxidant capacity of *D. kotschyi*. In addition, upregulation of enzymes rosmarinic acid synthase (RAS) and phenylalanine ammonia-lyase (PAL) was recorded. Vafadar et al. (2021) explored the effect of different concentrations of melatonin and Ca^{2+} on the photosynthesis and salt tolerance of *D. kotschyi*. The results showed that the best concentrations for enhancing growth, photosynthesis, and reducing MDA content under salinity stress were 5 mM $CaCl_2$ and 100 μM MT, respectively. The study suggested that melatonin-induced effects were mediated through calcium/calmodulin signalling. Cisse et al. (2021a) investigated the efficacy of exogenous application of melatonin and glycine betaine (GB) in providing salt tolerance to *Dalbergia odorifera*. Treatment of glycine betaine and melatonin increased the relative water content, growth parameters, chlorophyll and carotenoid content, transpiration, and net photosynthetic rate. Significant enhancement in concentration of antioxidant enzymes (SOD, GPX, AOX) and their activity was also observed in the treated seedlings.

12.4.2.2 Temperature

Extremes in temperature are an important environmental factor that causes significant damage to forest plants; it hinders the growth and developmental processes in plants by altering their physiology, membrane fluidity, and enzyme activities (Bhandari and Nayyar 2014; Szymańska et al. 2017). Photosynthesis is the principal biological process altered by cold and heat stress. It reduces photosynthetic capacity, chloroplast development, and chlorophyll fluorescence (Rehaman et al. 2021; Hassan et al. 2022).

Zhao et al. (2011) evaluated the effect of melatonin application in alleviating stress during cryopreservation of callus of *Rhodiola crenulata*, an important medicinal herb of alpine forests. The melatonin treatment prior to liquid nitrogen freezing significantly increases the survival of the cryopreserved callus. Uchendu et al. (2013) successfully cryopreserved the dormant winter buds and shoot tips of plantlets of *Ulmus americana* in liquid nitrogen under controlled environment after treating with melatonin and cold acclimation. Approximately 80–100% of shoot explants and all of the buds grew in melatonin-enriched media, demonstrating the usefulness of melatonin against chilling stress and long-term storage of germplasm of *U. americana*. Pu et al. (2021) found that exogenous melatonin and Ca^{2+} administration enhanced growth and relieved injuries in *Dalbergia odorifera* seedlings by regulating antioxidant enzymes and phytohormones, making the seedlings more tolerant against chilling stress. Exogenous melatonin and Ca^{2+} improved growth traits and reduced injuries in *D. odorifera* seedlings. Melatonin and Ca^{2+} enhanced photosynthetic activity and solute accumulation while reducing starch degradation induced by cold stress. They also enhanced antioxidant activities and increased the levels of GA3 and IAA while decreasing ABA levels.

12.4.2.3 Drought

Drought causes the photosynthetic apparatus to malfunction, which lowers the rate of photosynthetic electron transport, transpiration, stomatal conductance, and photosystem II efficiency. Drought stress results in membrane lipid peroxidation, cell membrane structural damage, electron leakage, and cell metabolism disruption, as well as damaged proteins and nucleic acids (Wang et al. 2017; Ahmad et al. 2019). Melatonin treatment reduces leaf senescence while also significantly increases PSII efficiency and boosts antioxidant enzyme activity (Sharma and Zheng 2019).

Exogenous melatonin application was found to improve the drought tolerance of *Perilla nankinensis* seedlings by increasing the relative water content and activity of antioxidant enzymes, viz. SOD, POD, and decreasing malondialdehyde content (Li et al. 2018). Wang et al. (2019) found that melatonin promotes the activity of the antioxidant enzyme system in *Carya cathayensis* (Chinese hickory) seedlings under drought stress. Significant improvement was observed in various parameters related to physiology and photosynthesis, viz. relative water content, rate and efficiency of photosynthesis and transpiration, stomatal conductance, and electron transport rate of PSII. Melatonin also stimulated the antioxidant apparatus by enhancing the activities of enzymes (SOD, CAT, APX); melatonin upregulated the expression of genes regulating these enzymes. In a similar study, Sharma et al. (2020) observed that exogenous application of melatonin improved the growth and photosynthetic efficiency of grafted Chinese hickory plants under drought. Melatonin also enhanced the antioxidative defence system and the accumulation of compatible solutes. Metabolomics analysis showed that melatonin modulated important metabolic pathways, including chlorophyll and carotenoid biosynthesis, sugar metabolism, and carbon fixation. Melatonin had a significant effect on the regulation of important genes that are involved in processes such as chlorophyll metabolism, antioxidative defence, and phenylalanine ammonia-lyase. Additionally, melatonin showed crosstalk with other hormones to regulate physiological processes. Cisse et al. (2021b) investigated the effects of Ca^{2+} associated with melatonin on seedlings of *Dalbergia odorifera* under drought stress. The results showed that this treatment improved growth traits and photosynthesis under normal as well as under stress conditions. Additionally, the Ca^{2+}-melatonin treatment decreased superoxide anion, lipid peroxidation, and relative conductivity and increased antioxidant activity, carbohydrates, and protein contents. Antioxidant systems were significantly increased by both Ca^{2+} and melatonin treatments, with the collective treatment showing better results. Overall, these studies suggest that melatonin treatment can ameliorate drought stress in forest plants by improving various physiological and biochemical parameters.

12.4.2.4 Heavy Metal Toxicity

Heavy metal toxicity is a serious abiotic stress that can significantly impair plant growth and productivity, affecting various stages of the plant's life from juvenile stage to maturity. Several research articles have demonstrated the effect of exogenous melatonin in alleviating heavy metal stress (Hoque et al. 2021). Yer (2022) assessed the effect of exogenous melatonin application on seed germination in *Pinus brutia* (Red Pine) under Cadmium stress. Melatonin acted in dose-dependent manner; at low concentrations it had favoured seed germination, while high doses it showed the negative impact.

12.4.2.5 UV Exposure

Ultraviolet radiation (200–400 nm) is categorised into three types: UV-C (200–280 nm), UV-B (280–320 nm), UV-A (320–400 nm). Among these UV-B (1.5% of total radiation) causes severe damage various physiological processes related to plant growth and development (Nawkar et al. 2013). Plants growing in habitats experiencing high levels of UV radiation, such as Alpine and Mediterranean regions, exhibit greater levels of melatonin as compared to their counterparts growing in areas with lower exposure to UV (Simopoulos et al. 2005). Afreen et al. (2006) investigated the concentration of melatonin in different tissues and developmental stages of *Glycyrrhiza uralensis* plant and its response to different light spectra and UV-B radiation. The results showed that root tissues contained the highest melatonin concentration and it increased with age. Red light exposed plants had the highest melatonin concentration, followed by blue and white light exposed plants (Table 12.2). Plants that received high-intensity UV-B radiation for a period of three days followed by low-intensity UV-B radiation for 15 days exhibited the highest concentration of melatonin suggesting that synthesis of melatonin in plants is linked to the intensity and duration of UV-B radiation.

12.5 Conclusion and Future Thrust

The adverse environmental conditions lead to alternation in many physiological processes of plants, which hamper their growth and development, resulting in a major reduction in productivity of forests. Melatonin is a pleiotropic signalling molecule known for protection of plants against variety of abiotic and biotic stresses.

Table 12.2 Melatonin functioning in forest plants under different stress conditions

Stress type	Plant species	Melatonin dose	Response by plant	References
Abiotic stress				
Saline-alkali stress	*Populus cathayana* × *canadensis*	50–800 µM	Melatonin concentrations of 50 µM and 100 µM significantly reduced the saline-alkali stress and were more effective than higher doses	Song et al. (2022)
Salt stress	*Betula platyphylla*	100–400 mmol/L	Melatonin worsens the effects of salt stress on germination characteristics of seeds	Li et al. (2017)
	Dracocephalum kotschyi	100 µM with 5 mM Ca^{2+}	Recovered plant growth, enhanced antioxidant enzyme activity, improved membrane integrity, reduced H_2O_2 and MDA content	Vafadar et al. (2020a)
			Enhanced production of phenolics, improved antioxidant capacity, upregulated PAL and TAL activities	Vafadar et al. (2020b)
			Increased shoot dry weight, leaf area, photosystem II efficiency, chlorophyll content, tolerance index, membrane stability, and stomatal conductance	Vafadar et al. (2021)
	Stevia rebaudiana	75, 150 µM	Stimulated plant growth by enhancing antioxidant activity, proline amount, carbohydrates content	Normohammadi et al. (2021)
	Dalbergia odorifera	0.05 and 0.1 mM	Decreasing the ROS, EL, and MDA; promoted the antioxidant activities	Cisse et al. (2021b)

(continued)

Table 12.2 (continued)

Stress type	Plant species	Melatonin dose	Response by plant	References
Temperature stress	*Datura metel*	Endogenous melatonin	Endogenous melatonin level increased young buds. Protection of reproductive tissues during development	Murch et al. (2009)
	Pinus nigra subsp. *pallasiana*	250, 500, 1000, and 1500 µM	Improved seedling growth and resistance to low temperature	Çelik et al. (2023)
	Rhodiola crenulata	0.1 µM	Increased survival of cryopreserved callus, peroxidase and catalase activity and reduced malondialdehyde production	Zhao et al. (2011)
	Ulmus americana	0.1–0.5 µM	Successful cryopreservation of dormant buds and shoot tips of in vitro grown plantlets	Uchendu et al. (2013)
	Dalbergia odorifera	MT and Ca^{2+}	Improved growth parameters and relieved injuries; enhanced antioxidant activities	Pu et al. (2021)
Drought stress	*Carya cathayensis*	25, 50, 100, and 200 µM	Improved seedling growth and various physiological process, viz. net photosynthetic rate, electron transport rate of PSII, maximum photosynthetic efficiency, transpiration rate, and stomatal conductance	Wang et al. (2019)
		0, 25, 50, 100, and 200 µM	Improved photosynthesis, antioxidant system, and regulated gene expression and metabolic pathways in grafted plants	Sharma et al. (2020)

(continued)

Table 12.2 (continued)

Stress type	Plant species	Melatonin dose	Response by plant	References
	Dalbergia odorifera	MT with Ca^{2+}	Increased growth traits and photosynthesis by improving water status, antioxidant systems, increasing GA3 and ZR, and decreasing ABA concentration	Cisse et al. (2021b)
	Salvia nemorosa and *salvia reuterana*	50, 100, 150, 200 µM	Alleviated oxidative stress by enhancing the activities of antioxidant enzymes (GT, CAT, POD, SOD, and GR); improved concentration and build of the essential oil	Bidabadi et al. (2020)
Heavy metal (cd) toxicity	*Pinus brutia*	25, 100, 150, 250, 1000, 2000 µM	Improved seed germination at low concentrations, while at high doses it showed the opposite effects	Yer (2022)
UV exposure	*Glycyrrhiza uralensis*	Endogenous melatonin	Elevated levels of endogenous melatonin on exposure to UV-B radiation	Afreen et al. (2006)
Biotic stress				
Beetle *(Scolytus multistriatus)* feeding	*Ulmus americana*	Endogenous melatonin	Spike of about 7000 times in melatonin in the saplings	Saremba et al. (2017)
Leaf diseases	*Panax notoginseng*	10 µM	Increased accumulation of endogenous melatonin by upregulation of genes involved in its biosynthesis; 40% decrease in the incidence of leaf diseases compared to the control	Yang et al. (2021b)

(continued)

Table 12.2 (continued)

Stress type	Plant species	Melatonin dose	Response by plant	References
Pseudomonas syringe			Induced stomatal closure thus helped prevent the invasion of pathogen by activating MAPK and NADPH oxidase-mediated ROS production	Yang et al. (2021a)

ABA abscisic acid, *CAT* catalase, *EL* electrolyte leakage, *GA3* gibberellic acid 3, *GR* glutathione reductase, *GT* glucosyltransferase, H_2O_2 hydrogen peroxide, *MAPK* mitogen-activated protein kinase, *MDA* malondialdehyde, *NADPH* nicotinamide adenine dinucleotide phosphate (reduced form), *PAL* phenylalanine ammonia-lyase, *POD* peroxidase, *ROS* reactive oxygen species, *SOD* superoxide dismutase, *TAL* tyrosine ammonia-lyase, *ZR* zeatin riboside

Its diverse roles and potential applications in agriculture have been explored on wider extent, and now it is important to translate this knowledge in reference to forestry species. Applying the finding from agricultural and horticultural research to forest plants can expand our understanding of melatonin's function and potentially help us to improve growth, productivity, and stress tolerance in forestry species.

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Melatonin: A Promising Tool Against Climate Change and Food Security for Better Plant Survival

13

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Abstract

Global population is increasing day by day creating a challenge for agriculturists to meet the global food demand. Climate change is an obstacle that hinders plant growth leading to reduced food production. Use of chemical fertilization has resulted in poor plant nutrient use efficiency and land degradation. In the scenario, it is important to find a promising tool against climate change and food security for better plant survival. Melatonin has potential to increase plant growth, improve crop yield, help plants to resist and survive against environmental stresses including salt, drought, temperature, and metal toxicity. It improves various functions in plants, acts as an antioxidant, regulates gene expression, contributes in metabolism of plant hormones. The exogenous application of melatonin also has a potential to improve plant production and protection. This chapter focuses on the discussions about the influence of melatonin in competing food security and climate change challenge, whereas mechanism behind its functionality needs to be addressed in future studied.

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Keywords

Abiotic stress · Antioxidant · Plant hormone · Heavy metal · Growth regulator

13.1 Introduction

Melatonin (N-acetyl-5-methoxytryptamine) is an endogenous indolamine naturally occurring in evolutionarily distant organisms (Nawaz et al. 2020). It was first isolated from the bovine pineal gland in 1958 having density of 1.269 g cm^{-3} and molecular mass of 232.28 g mol^{-1}. It plays a role in reversing the effect of melanocyte-stimulating hormone, thus named as melatonin. European Chemicals Agency (ECHA) reports that melatonin has no classified hazards (Agathokleous et al. 2021). Melatonin naturally occurs in plants, animals, and algae but its concentration is much higher in plants as compared to animals. Unlike this, its biosynthesis in plants is more complicated than in animals; therefore, its definitive pathway occurring in plants is still undefined (Nawaz et al. 2016).

Melatonin has diversified roles in plant growth and development including seed germination and protection, root development, and fruit ripening (Zhao et al. 2019) and also improves photosynthesis in plants leading to delayed senescence. In addition, it also contributes in modulating gene expression and metabolism of plant hormones such as auxins, abscisic acid, cytokinin, ethylene, and gibberellins. It also has a capacity to control reactive oxygen and nitrogen species, regulate antioxidant enzymes, and improve the electron transport chain in mitochondria, thus reducing electron leakage (Nawaz et al. 2020). It also develops defense mechanism in plants against biotic and abiotic stresses (Arnao and Hernández-Ruiz 2015).

In this chapter, we have aimed to understand the role of melatonin as a tool to tackle climate change and food security. The chapter consists of five sections, which describes the introduction (Sect. 13.1), challenges and relation between food security and climate change (Sect. 13.2), potential roles of melatonin to the plant ecosystem (Sect. 13.3) that is further classified into plant nutrition, phytoremediation, and environmental stresses, constraints, challenges, and future aspects (Sect. 13.4), and the conclusion (Sect. 13.5), respectively.

13.2 Challenges and Relation Between Food Security and Climate Change

Climate change and food security are the two major issues that directly relate to agriculture sector (Chandio et al. 2020). Therefore, this section needs huge attention and openly challenges the scientists and agriculturalists to deal with it maintaining agricultural sustainability and serve mankind. The world population is increasing day by day and it is estimated to reach 9.7 billion by 2050 leading to an increase in food demand. To feed this growing global population, nearly 70% increase in food production will be required (Raza et al. 2022). Before stepping into the accomplishment and tactics to achieve this high food demand, here it is important to understand the concept of food security. Food security is defined as adequate access to food in quality and quantity aspects. In the last two decades, food security is categorized into four main dimensions (Iriti and Vitalini 2020):

1. Supply: Availability of enough quantity of food of suitable quality.
2. Economic: Food access depending upon the income and prices.
3. Consumption: Utilization of food through adequate diet and reach the state of nutritional well-being.
4. Stability: The constancy of the above 3 dimensions over time.

Application of increased agrochemicals has been practiced extensively to achieve food security dimension, high food demands, and increase plant growth and production. However, agricultural inputs act as plant growth regulators and plant nutrients but its excessive use has contributed a lot toward land degradation and environment deterioration (Tijjani and Khairulmazmi 2021). Excessive use of nitrogen (N) fertilizers results in reduced N-use efficiency in plants, eutrophication, nutrient pollution, and greenhouse gases emission (Yang et al. 2015). Moreover, the conventional methods adopted to improve rice yield using chemical fertilizers result in higher nitrate (N_2O) emissions and global warming (Abbhishek et al. 2022).

The anthropogenic greenhouse gases emissions have adversely changed the global climate resulting in warmed oceans and atmosphere causing lesser amount of ice and snow and higher sea levels (Iriti and Vitalini 2020). A study reported that land-use related carbon dioxide (CO_2) emissions contribute to almost 14% of annual anthropogenic CO_2, out of which 10% comes from agriculture (Abbhishek et al. 2022). This increasing global warming, climate change, and environmental pollutions will negatively impact the crop yields and will be a hurdle in achieving agriculture food demands to feed the global population (Agathokleous et al. 2021).

13.3 Potential Roles of Melatonin to the Plant Ecosystem

Exogenous application of melatonin has resulted in positive results on plants and their edible parts, and algae. A meta-analysis reported that exogenous application of melatonin has a potential to regulate diverse biological functions in plants leading to increased plant yield and production and improve its nutritional and nutraceutical value even under current climate change scenarios (Agathokleous et al. 2021). It also plays a significant role in modulation gene expressions of phyto-hormones and promote plant growth. For instance, melatonin acts like auxins and contributes to improved growth of lateral and adventitious roots (Nawaz et al. 2020).

According to a meta-analysis, it plays an important role in improving plant growth, gas exchange parameters, antioxidant enzyme activities photosynthetic pigments, protein and soluble sugar levels in plants (Muhammad et al. 2022). Another study reported that melatonin when applied on Brassica rapa seedlings promoted its vegetative growth by improving rate of cyclic electron flow around photosystem (PS) I, electron transport efficiency, and fluorescence quantum yield (Teng et al. 2022). Moreover, melatonin can improve the indoleamine levels in plants promoting crop production. This nutritional status of crops can be achieved either through seed priming or transgenic methods (Tan et al. 2012).

Melatonin acts as a plant growth regulator and helps plant to develop resistance against environmental stresses including salinity, drought, temperature as well as heavy metals. Each of them is discussed below:

13.3.1 Melatonin: Environmental Stress

The natural habitat gives tremendous challenges to plants due to detrimental environmental factors. Therefore, plants develop a complex immune system to deal with such adverse conditions. Various plant hormones and bio-stimulators play an important role in developing abilities in plants to deal with such adverse environmental stresses, melatonin is one of them (Fig. 13.1). It has a potential to boost the physiology of plant and acts as an antioxidant compound. Plant faces multiple

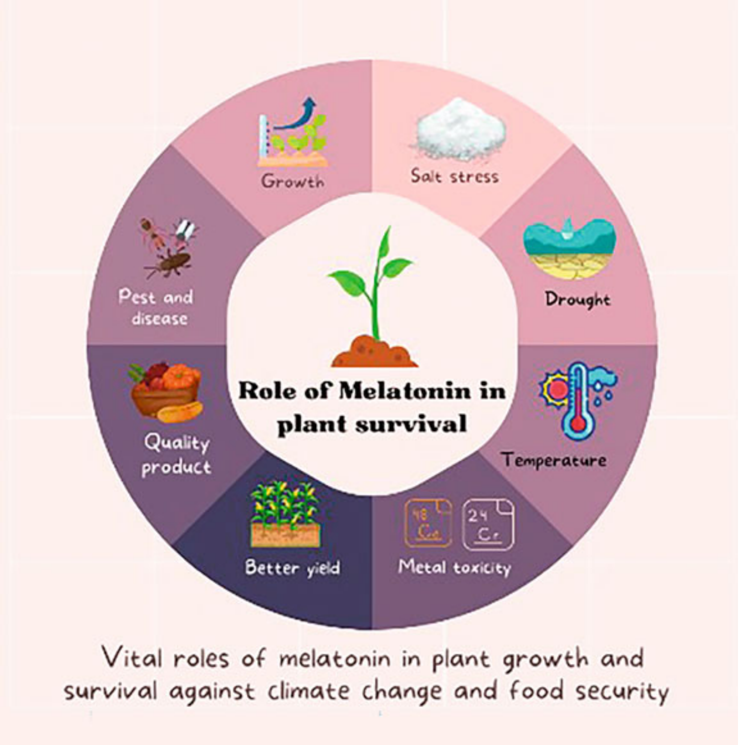

Fig. 13.1 Vital roles of melatonin in plant growth and survival against climate change and food security

environmental stress as compared to animals due to their sessile nature. Under stress condition, plants unregulate melatonin production that helps them fight against oxidative stress occurred (Zhao et al. 2019). Salt stress is one of the serious plant growth limiting factors globally and adversely reduces crop yield annually. The plants facing salt stress have lower photosynthetic rate, higher ROS, and disrupt ion homeostasis leading to poor plant growth (Zhan et al. 2019).

Melatonin acts as signaling molecule linked with defense mechanism against environmental stresses including cold, drought, and salt stress and helps plant in stimulating its growth and development (Nawaz et al. 2020). Exogenous application of melatonin can pass through the plasma membrane increasing the endogenous concentration of melatonin, thus helping plant grow better in salt stress conditions (Li et al. 2019). A study reported that cucumber seedlings when treated with melatonin improved cell viability, enhanced antioxidant enzyme activity, improved photosynthesis, inhibited active oxygen explosion, and reduced malondialdehyde relative conductivity and concentration under salt stress (Zhang et al. 2020). In addition, exogenous melatonin alleviated salt stress in rice seedlings by promoting photosynthesis (Yan et al. 2021), wheat seedling by modulating polyamine metabolism (Ke et al. 2018), and in watermelon by improving photosynthesis and redox homeostasis (Li et al. 2017).

Drought is another serious threat to crop growth causing several anatomical, morphological, physiological, and biochemical abnormalities in plants. It reduces plant photosynthetic rates, accelerates leaf senescence, degrades chlorophyll contents, disturbs water and nutrient use efficiency, and causes oxidative damage to cell membrane (Tiwari et al. 2021). Melatonin has the potential to protect plant from these damages by improving antioxidant defense activity and ROS scavenging in plants (Sharma and Zheng 2019). A study demonstrated that melatonin application enhanced reduced ROS-induced oxidative damages by increasing chlorophyll content, relative water content, osmo-protectants, and antioxidant enzyme activities of maize seedlings when melatonin was applied as soil drench (Ahmad et al. 2021). Similar findings were reported in soybean with foliar or root treatment (Imran et al. 2021), tomato plants (Altaf et al. 2022; Ibrahim et al. 2020), and wheat seedlings with foliar treatment (Cui et al. 2017).

A serious threat is expected in the near future for food security and plant production due to drastic change in climate, increase in temperature, and reduction in rainfall. Heat stress alters the plant enzyme activity, disturbs plant photosynthetic efficiency, membrane integrity, damages plant molecules including lipids, proteins, and deoxyribonucleic acid (DNA; Hassan et al. 2022). The studies reported that melatonin contributed in improved plant growth under heat stress environment (Buttar et al. 2020; Xu et al. 2016).

13.3.2 Melatonin: Heavy Metals

Accelerated industrialization has recently contributed significantly to environmental contamination by releasing significant amounts of hazardous metals, notably nickel

(Ni), into the ecosystem (Rizwan et al. 2018). Heavy metals pose a serious environmental and nutritional problem due to their inability to degrade. Their accumulation decreases the normal growth and development process. Therefore, they cause acute poisoning and even death of living organisms. Melatonin is a prime beneficial molecule in protecting plant from oxidative stress because of its potential to directly eliminate reactive oxygen species (ROS). As plants are sessile, they must survive a variety of stressors during their life cycle. In order to live in a hostile environment, plant cells must undergo quick and massive transformation (Chem et al. 2021).

Heavy metals such as zinc (Zn) and copper (Cu) are required for normal plant growth, but excessive amounts are poisonous. In enzymes and other proteins, the metal ion attaches to the sulfhydryl group, by limiting their activity or changing their structure (Shen et al. 2013). Moreover, heavy metals also induce oxidative damage to biomolecules by initiating free radical-mediated chain reactions that culminate in lipid peroxidation, protein oxidation, and nucleic acid oxidation (Zhang et al. 2014). Metals also have harmful effects in that they enhance the creation of ROS, which disrupts the cell's redox homeostasis (Namdjoyan and Khavari-Nejad 2011). Moreover, adding melatonin to soil improved the tolerance and survival of pea plants (*Pisum sativum* L.) to Cu contamination, showing that the presence of melatonin in plants can be employed in phytoremediation (Tan et al. 2007).

The use of melatonin to boost the phytoremediative capacity of various plants could be a viable and cost-effective approach to combating environmental contamination (Moradkhani et al. 2010). By treating *Galinsoga parviflora* with 100 M melatonin is the improved remediation efficiency of cadmium (Cd) contaminated soil. Melatonin improved the transfer of Cd from roots into shoots of this plant species. Potato weed is a Cd hyper-accumulator and has a high tolerance to it. Melatonin not only increased the activity of antioxidant enzymes under low Cd concentrations, but it also increased the transfer of Cd to the cell wall and vacuoles, removing Cd from sensitive parts of the cell and accelerating its absorption (Tang et al. 2018).

Melatonin is abundant throughout the plant kingdom but varies greatly from species to species. Its high levels may assist plants fight against environmental stress caused by water and soil contaminants. The reported content ranges from a few pg g^{-1} tissues to many mg g^{-1} tissue (Tan et al. 2007). As a result, cleanup of the Cd-contaminated soil is critical. Phytoremediation is one of the technologies for remedying heavy metal contaminated soil and has various advantages such as low cost, high efficiency, and lack of secondary pollutants compared with the physical or chemical remediation approaches (Brown et al. 1995). Exogenous melatonin has also been demonstrated to be effective in reducing the harmful effects of heavy metals in plants (Tan et al. 2007).

Melatonin can reduce heavy metal accumulation in plants under heavy metal contaminated circumstances by boosting plant resistance (Li et al. 2016). It may improve plant resistance to harsh environmental conditions by slowing chlorophyll breakdown, boosting antioxidant defense, and decreasing heavy metal buildup (Chaoqiang and Chaolong 2015). Melatonin-mediated stress tolerance mechanisms under heavy metal stress are primarily associated with the modulation of antioxidant activity and related gene expression, as well as the scavenging of excess ROS (Nabaei and Amooaghaie 2019). Plants build more glutathione and phytochelatins to chelate excess heavy metals after melatonin treatment, improving cell wall trapping (Cao et al. 2019).

13.4 Constraints, Challenges, and Future Aspects

Various functions of melatonin in promoting plant growth and development have been reported but still there are some limitations and research gaps that need to be addressed in future. We found the capabilities of melatonin under various stresses but its role in combination with synthetic fertilizers and other signaling molecules is still unknown. In addition, the response of plants against melatonin and its interaction with nutrients transportation and uptake needs attention. Furthermore, limited data is available describing the response of plants to folia application of melatonin.

Exploring the benefits and functionality of melatonin is not enough but the scientific community has to find out the mechanisms behind action, melatonin receptors and melatonin interacting proteins, signaling pathways, and characterization of melatonin signaling cascades. Moreover, distribution of melatonin in various plant organs and their specific role in respective organ needs investigation. Literature reported that melatonin acts as auxins but its involvement and interaction with auxins should be examined for better understanding. The short term and long term impacts of melatonin application on plants on small scale and field conditions should be studied. The studies should not be limited to cereal or medicinal crop, and different varieties, species, application time, and doses should be examined under different soil and environmental conditions for exploring the benefits of melatonin in sustainable agriculture. Scientists and agriculturists are performing multiple researches to find the potential of melatonin and we will surely find new insights in future contributing to better crop production, safer environment, and food security.

13.5 Conclusion

Climate change is defined as the shift in climate patterns due to anthropogenic activities causing greenhouse gases emission and global warming. It is a major hurdle in achieving food demand for the increasing global population. Excessive use of chemical fertilizers results in land deterioration and environmental pollution. Therefore, exploring an alternative with better results and lesser hazards needs to be explore. Melatonin is promising against climate change and food security for better plant survival. It is an eco-friendly and economic strategy against environmental stresses (drought, chilling, heavy metal, salt) for improved crop production. In addition, melatonin has potential in improving plant growth and development, plant physiological and biochemical mechanism, quality of edible products, feed products and its quality and enhancing plant yield even under harsh climatic conditions and environmental pollution factors. All such functions make melatonin an antioxidant and immunity booster for plants. Besides this, the mechanisms behind its application and its long term impacts, large scale application, timing and doses for specific crops, and its relation to other hormones still need investigation. In conclusion, melatonin can boost the plant performance even under stress conditions leading to achieving better and safe food supply. Availability of this product to the small scale farmers and the crop growers will be helpful in the long run.

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