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Milan Kumar Lal  
Rahul Kumar Tiwari *Editors*

# Melatonin in Plants: A Pleiotropic Molecule for Abiotic Stresses and Pathogen Infection

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Editors

# Melatonin in Plants: A Pleiotropic Molecule for Abiotic Stresses and Pathogen Infection

 Springer

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## Preface

Recent years have seen a transformative renaissance in our understanding of melatonin's pivotal role in plant biology as a pleiotropic molecule. Initially recognized for its involvement in circadian rhythms and neuroendocrine regulation in animals, melatonin has captured the fascination of the scientific community due to its presence and multiple functions in plants. A pleiotropic molecule for abiotic stresses and pathogens, *Melatonin in Plants* depicts the complex interplay between melatonin and plant responses to abiotic stresses and pathogens. The chapters contained in this volume are the culmination of meticulous research and scholarly inquiry conducted by esteemed scientists and researchers who have dedicated themselves to unraveling the diverse roles of melatonin in plants. A comprehensive exploration of melatonin's effects on a variety of physiological processes, particularly plant responses to abiotic stressors and the activation of defense mechanisms against pathogens, is the purpose of this compendium.

An in-depth understanding of the intricate molecular pathways of melatonin in plants is provided in the first section of the book. The following chapters present cutting-edge investigations into the pleiotropic effects of melatonin on plant responses to abiotic stresses, including drought, salinity, extreme temperatures, and heavy metal toxicity. The ability of melatonin to ameliorate the adverse effects of these environmental adversities reveals its potential as a potent bio-regulator for enhancing plant resilience. Moreover, the book describes how melatonin plays an important role in plant-pathogen interactions, revealing how it primes plant defense systems against a wide range of pathogens. These chapters provide compelling evidence of melatonin's importance in reducing the detrimental effects of plant diseases and improving global food security by elucidating the mechanisms through which it enhances plant immunity.

In exploring the frontiers of melatonin research in plants, we invite readers on a journey of scientific discovery, enriched by multiple perspectives and methodologies. Our sincere hope is that this compilation will serve as an invaluable resource for students, researchers, and practitioners in the fields of plant biology, agriculture, and environmental science, inspiring further inquiry and application of melatonin-based strategies for sustainable agriculture and ecosystem management. Those who contributed to this pioneering compilation have shown unwavering dedication, expertise, and passion, and we are deeply grateful to them. Their

collective efforts have highlighted the profound role played by melatonin as a pleiotropic molecule in orchestrating the delicate balance between plant survival and adaptation in a dynamic and challenging environment.

As a contribution to the advancement of plant science and sustainable agriculture, we present *Melatonin in Plants: A Pleiotropic Molecule for Abiotic Stresses and Pathogens*. In order to harness the potential of melatonin in strengthening plant resilience and ensuring a fruitful, secure future for our planet, I hope the knowledge and insights shared in this volume inspire new avenues of research.

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Shimla, Himachal Pradesh, India  
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**Muhammad Ahsan Altaf** completed his Ph.D. from the School of Life Science at Hainan University, China. He is currently employed as a postdoctoral researcher in the College of Horticulture, Hainan University, China. He has published around 50 research articles in top leading journals of the world, having high impact factor. His research interests are focused on the physiological, biochemical, and molecular aspects of horticultural plants, especially solanaceous vegetable crops. Dr Altaf is actively engaged in investigating the role of melatonin in photosynthetic efficiency and mineral nutrient uptake from root to shoot under 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

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**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. His 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

$^1\text{O}_2$	Singlet oxygen
ABA	Abscisic acid
AMT	Ammonium transporters
APX	Ascorbate peroxidase
ATP	Adenosine triphosphate
CAT	Catalase
CBFs	C-repeat-binding factors
CKs	Cytokinins
COMT1	Caffeic acid o-methyltransferase 1
CRISPR	Clustered regularly interspaced short palindromic repeats
CWI	Cell wall invertase
DHAR	Dehydroascorbate reductase
EC	Electrical conductivity
ETIs	Effector-triggered immunity
FAD2	Fatty acid desaturase
GA	Gibberellin
GABA	Gamma-aminobutyric acid
GM	Gene manipulation
GPX	Glutathione peroxidase
GR	Glutathione reductase
GSH	Glutathione
$\text{H}_2\text{O}_2$	Hydrogen peroxide
HM	Heavy metals
HSFs	Heat shock transcription factors
HSPs	Heat shock proteins
IAA	Indole-3-acetic acid
JA	Jasmonic acid
MAPK	Mitogen-activated protein kinase
MDA	Malondialdehyde
MDHAR	Monodehydroascorbate reductase
MEL	Melatonin
MIR	Melatonin-mediated induced resistance
NBS-LRR	Nucleotide-binding site leucine-rich repeat

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NiR	Nitrite reductase
NO	Nitric oxide
PAL	Phenylalanine ammonia-lyase
PAMPs	Pathogen-associated molecular patterns
POD	Peroxidase
PSI	Photosystem I
PSII	Photosystem II
PTI	PAMP-triggered immunity
QTL	Quantitative trait loci
RNS	Reactive nitrogen species
ROS	Reactive oxygen species
RWC	Relative water content
SA	Salicylic acid
SAMDC	S-adenosylmethionine decarboxylase
SAR	Systemic acquired resistance
SNAT	Serotonin N-acetyltransferase
SOD	Superoxide dismutase
T5H	Tryptamine 5-hydroxylase
TDC	tryptophan decarboxylase
TPH	Tryptophan hydroxylase
ZFPs	Zinc finger proteins



# Evolution of Melatonin as an Oxidative Stress Mitigator in Plant

1

Rahul Kumar Tiwari, Muhammad Ahsan Altaf, Ravinder Kumar, and Milan Kumar Lal

## Abstract

In diverse crop plants under a variety of adverse conditions, melatonin, a versatile and potent molecule, plays a significant role in reducing oxidative stress. A number of studies have demonstrated its ability to mitigate various abiotic stresses, such as drought, extreme temperatures, and salinity. As an antioxidant, melatonin plays a crucial role in this context. The antioxidant properties of melatonin reduce the oxidative damage caused by reactive oxygen species to cellular components, such as lipids, proteins, and nucleic acids. By protecting cellular membranes and enhancing their functionality, it enhances plant resilience under stress. Furthermore, melatonin promotes carbohydrates metabolism under stress conditions by increasing photosynthetic efficiency. It preserves the process of converting light energy into carbohydrates by safeguarding the photosynthetic machinery. The protection provided by photosynthesis ensures the availability of energy and metabolic intermediates for growth and development, regardless of the environmental conditions. Also, melatonin affects carbohydrate metabolism, carbon assimilation, and ATP synthesis by modulating enzyme activity. In addition, it influences sugar transport, which is crucial to carbohydrate metabolism and overall energy distribution, particularly during times of stress. Overall,

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melatonin is an important mitigator of oxidative stress in crop plants. As a valuable tool for improving stress resilience and productivity in agriculture, melatonin is capable of combating oxidative damage, maintaining photosynthetic efficiency, and modulating carbohydrate metabolism. In an era of increasing environmental stress, further research into its mechanisms and potential applications could be highly advantageous.

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**Keywords**

Carbohydrate metabolism · Lipid peroxidation · Redox · Ionic homeostasis · Reactive species

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## 1.1 Introduction

Melatonin (N-acetyl-5-methoxytryptamine) is a versatile plant regulator found in all living organisms (Hernández-Ruiz and Arnao 2018; Altaf et al. 2023). It was originally identified as a neurohormone secreted by the pineal gland in vertebrates (Lee et al. 2003). As a vital animal hormone involved in circadian rhythms, body temperature, appetite, sleep, the immune system, seasonal reproduction, and tumorigenesis, melatonin is now recognized as one of the most important hormones. Two independent research groups discovered melatonin in plants (Dubbels et al. 1995; Hattori et al. 1995) and this led to significant research into melatonin extraction, quantification, and physiological functions (Tan and Reiter 2020; Tiwari et al. 2020a, 2021b, 2022; Altaf et al. 2022b, 2023). The term “phytomelatonin” was introduced in 2004 to refer to plant-derived melatonin, and subsequent studies have established its diverse functions in regulating plant growth, seed germination, cell respiration, photosynthesis, and osmoregulation (Reiter et al. 2009; Tan and Reiter 2020). In addition to stimulating rhizogenesis, morphogenesis, and caulogenesis, melatonin also plays an important role in caulogenesis. Plants use melatonin as a phytoprotectant against various abiotic stresses, which is one of its most important roles. It has been found that it reduces the effects of drought and heat (Wei et al. 2017; Buttar et al. 2020; Jahan et al. 2021), salinity (Altaf et al. 2020; Li et al. 2012; Kostopoulou et al. 2015; Wang et al. 2016), cold (Bajwa et al. 2014; Ding et al. 2017a, b; Jannatizadeh 2019; Sharafi et al. 2019), and heavy metal toxicity (Kaya et al. 2020; Ahammed et al. 2020).

Climate change exposes plants to a wide range of biotic as well as abiotic stresses, which pose threats to their growth and productivity (Kumar et al. 2017, 2019, 2022a, b). There is a strong correlation between reactive oxygen species (ROS) and oxidative stress on a molecular level. As a result of biotic or abiotic stresses, ROS like hydrogen peroxide ( $H_2O_2$ ), singlet oxygen ( $^1O_2$ ), and superoxide radicals like hydroxyl radicals can accumulate in plants, including oxygen radicals and their derivatives, such as hydrogen peroxide ( $H_2O_2$ ) and singlet oxygen ( $^1O_2$ ) (Tiwari et al. 2020b, 2022). In addition to the fact that ROS are highly reactive, they can also cause damage to plants due to their toxic effects. During the oxidation process, ROS

can damage cells by oxidizing proteins, lipids, and DNA, which can result in the death of cells.

Recent studies have shown that ROS play an important role in early signaling events in plants, triggered by normal metabolic functions and environmental stressors (Tiwari et al. 2021a, 2022; Devi et al. 2022; Lal et al. 2022b; Mangal et al. 2022). ROS production and their elimination are delicately balanced under normal circumstances. There are, however, different biotic and abiotic stresses that can disrupt this balance, leading to significant increases in ROS levels that must be countered by antioxidant defense mechanisms within plant cells. It has become a critical objective for plant biologists to enhance these antioxidant defense systems in plants Kumar et al. (2021a, b).

By maintaining ionic homeostasis and preventing adverse effects such as cell membrane damage, protein and DNA denaturation, lipid peroxidation, carbohydrate oxidation, pigment breakdown, and aberrant enzyme activity, melatonin maintains ionic homeostasis and prevents reactive oxygen species (ROS) and reactive nitrogen species (RNS) generated during stress (Tan et al. 2007; Reiter et al. 2009; Moustafa-Farag et al. 2020). The plant's inherent antioxidative defense system is also activated by melatonin by upregulating genes that help produce enzymes like superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione peroxidase (GPX), ascorbic acid (ASA), and glutathione (GSH) when stressed (Sun et al. 2019). There is also evidence that upregulation of genes involved in the ASA-GSH cycle, which protects the plant against stress, is well established (Altaf et al. 2021a, b).

A number of previous studies have found that melatonin inhibits viral and fungal infections in animals both directly and indirectly (Vielma et al. 2014; Tiwari et al. 2021a). Numerous studies have demonstrated melatonin's ability to inhibit plant pathogens indirectly and elicit systemic acquired resistance in crops (Zhang et al. 2017; Zhao et al. 2019; Sun et al. 2019). The protective properties of melatonin have been demonstrated in plants against viruses, fungal pathogens, bacterial pathogens, insects, and parasitic nematodes in crops (Zhang et al. 2017; Zhao et al. 2019; Sun et al. 2019).

Plant defense is regulated by a number of processes, including activation of defense genes, scavenging of reactive oxygen species (ROS) and reactive nitrogen species (RNS), thickening of the cell wall, and hormonal interaction (Kumar et al. 2020; Altaf et al. 2022a; Behera et al. 2022; Devi et al. 2022; Lal et al. 2020, 2022c). Melatonin increases callose deposition and cellulose, galactose, and xylose accumulation in plants, leading to a series of biochemical defense responses against fungal pathogens (Sun et al. 2015; Qian et al. 2015). It has been reported that the melatonin-mediated systemic acquired resistance (SAR) is activated by salicylic acid (SA) and jasmonic acid (JA), which are crucial for preventing viral diseases (Tiwari et al. 2022; Altaf et al. 2023). Additionally, plant defense responses are induced by melatonin and serotonin working synergistically (Saremba et al. 2017). It is necessary to investigate further the molecular mechanism underlying this synergistic interaction, as this interaction has not yet been fully investigated. Phytomelatonin is well known and documented for its protective effects against abiotic stress, but the

effects on biotic tolerance have been less well recognized and documented. A greater understanding and appreciation of phyto-melatonin potential in plants facing biotic stress requires additional research. A major goal of this chapter is to explain how melatonin helps plants in mitigating pathogen infections and abiotic stresses through regulation of the antioxidative and oxidative defense systems. In addition, the chapter discusses how hormonal cross-talk is mediated by melatonin and influences the triggering of immune responses by PAMPs and ETIs. Furthermore, recent studies investigating the synergistic interaction between melatonin and other phytoprotectants are discussed, underscoring the potential of melatonin as a multi-functional phytoprotectant in sustainable crop production systems.

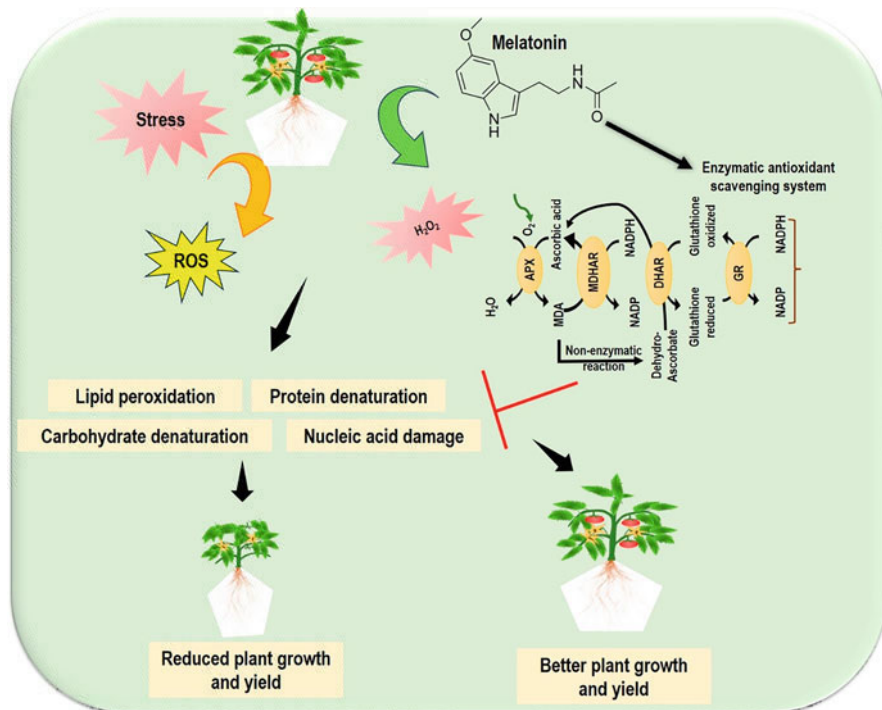
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## 1.2 Oxidative Stress: The Phenomenon and Associated Effects

Oxidative stress occurs when free radicals and reactive metabolites, known as oxidants, are produced in excess and their elimination is not balanced by protective mechanisms called antioxidative systems (Palma et al. 2002; Vielma et al. 2014). Damage to vital biomolecules and plant tissues and organs can result from this imbalance, potentially affecting the entire body. The redox state of cells and organisms is affected by oxidative and antioxidative processes (Reiter et al. 2009; Antoniou et al. 2017). By altering redox state, various signal proteins can be stimulated or inhibited, affecting signal pathways that impact cellular function. Many studies have shown that oxidative stress does not always damage cells. Oxidative stress can play a role in regulating other essential processes depending on the type of oxidant, the intensity and duration of redox imbalance, and the type of cell involved (Zhang and Zhang 2014; Miryeganeh 2021; Altaf et al. 2022a). Modulation of signal pathways, modulation of antioxidant enzyme synthesis, enhancement of repair processes, modulation of inflammation, and modulation of apoptosis (programmed cell death) are all part of this process. Physiological and pathological processes in the plants can be affected by the intricate balance between oxidative stress and cellular responses to it (Lei et al. 2004).

Oxidative stress is a general stress response that results in cell damage and dysfunction when environmental or biotic stresses are present. In reactive oxygen species (ROS), excess molecules containing activated oxygen are produced and accumulate, resulting in oxidative stress. Oxidative stress is caused by two main factors: Disruption of normal cell physiology causes an imbalance between ROS generation and detoxification. As part of the defense and adaptation process, ROS are synthesized *de novo* during stress signaling. Some stress factors directly produce ROS, contributing to oxidative stress, allowing both mechanisms to coexist (Demidchik 2012; Bian et al. 2021). Oxidative stress is induced by reactive oxygen species (ROS) in biological systems. There are several ROS that can be produced, including the singlet oxygen ( $^1\text{O}_2$ ), hydroxyl radicals (OH $\cdot$ ), hydrogen peroxide ( $\text{H}_2\text{O}_2$ ), superoxide radicals ( $\text{O}\cdot^{-2}$ ), and nitric oxide ( $\text{NO}\cdot$ ) (Demidchik 2012). Oxidative stress may also be caused by other ROS, such as peroxy, alkoxy, and hydroperoxy radicals, peroxynitrite, ozone, and hypochlorous acid.

Triplet oxygen ( $O_2$ ) can undergo a process where it loses its “spin restriction” by accepting a single electron. This electron acceptance can occur due to various reasons, such as the “leak” of electrons in the plant’s electron transport chain (ETC) or the functioning of NADPH oxidase. As a result of this process,  $O_2$  transforms into a highly reactive species known as superoxide radical ( $O\bullet^{-2}$ ). This radical is often referred to as “superoxide anion radical,” “superoxide radical anion,” “superoxide radical,” or simply “superoxide.” The increased reactivity of superoxide makes it an important player in oxidative stress and various biological processes (Chen et al. 2019; Allen 2003). In comparison with superoxide, hydroxyl, and singlet oxygen, hydrogen peroxide ( $H_2O_2$ ) is a weak acid without unpaired electrons. The lifespan of  $H_2O_2$  in living tissues is not overly long ( $<1$  s) due to the actions of catalases and peroxidases, which break down this substance (Chao et al. 2009; Chen et al. 2018). Contrary to the cytoplasm, which is highly reduced and antioxidant-rich, the extracellular space is acidic and lacks enzymes that can scavenge  $H_2O_2$ , including catalases and peroxidases, as well as superoxide dismutase, which removes its precursor. As a result of the limited activity of enzymatic ROS scavengers,  $H_2O_2$  accumulates in the apoplast, causing oxidative stress (Chen et al. 2018). During oxidative stress, the hydroxyl radical ( $\bullet OH$ ; Fig. 1.1) causes oxidative damage to proteins, nucleic acids, and lipids. It contributes directly to oxidative stress signaling and programmed cell death (Demidchik 2012). As a result of stress factors, this stimulates  $Ca^{2+}$  and  $K^+$  channels the most significantly in comparison to other ROS and free radicals, resulting in a rapid influx of  $Ca^{2+}$  and efflux of  $K^+$ . Within cells, singlet oxygen likely targets cytosolic signaling cascades, plasma membrane components, and tonoplast ion channels. A variety of cellular components and structures can be affected by this species modifying cytosolic signaling pathways, influencing plasma membrane ion channel activity, and altering tonoplast ion channels (Chang et al. 2014). Therefore, singlet oxygen can influence multiple cellular processes and contribute to oxidative stress. The presence of reactive nitrogen species (RNS) can result in oxidative stress. Nitric oxide ( $NO\bullet$ ), peroxynitrite ( $ONOO^-$ ), and nitrogen dioxide ( $\bullet NO_2$ ) are RNS molecules that contain nitrogen. The reactive nitrogen species (RNS) can cause oxidative damage to proteins, lipids, and DNA, similar to ROS (Mukherjee 2019; Rai et al. 2020; He and He 2020). The formation of peroxynitrite is a key mechanism through which RNS induces oxidative stress. During the reaction between nitric oxide and superoxide radical, peroxynitrite is formed, and it is a powerful oxidant that causes lipid peroxidation and protein modification to occur. Additionally, RNS can influence ROS generation and activity. Nitric oxide ( $NO\bullet$ ) can, for example, react with superoxide radicals to form peroxynitrite, but it also scavenges superoxide radicals, reducing their levels and indirectly affecting cellular redox balance.



**Fig. 1.1** A schematic model on melatonin mediated oxidative stress mitigation. APX Ascorbate peroxidase, DHAR Dehydroascorbate reductase, GR Glutathione reductase,  $H_2O_2$  Hydrogen peroxide, MDHAR Monodehydroascorbate reductase, NADP Nicotinamide adenine dinucleotide phosphate, NADPH Nicotinamide adenine dinucleotide phosphate hydrogen,  $O_2$  Oxygen, ROS Reactive oxygen species

### 1.2.1 Mechanism of Oxidative Stress: Oxidation of Lipids

As a result of oxidative stress, proteins, polynucleic acids, carbohydrates, and lipids undergo reversible or irreversible modifications, leading to the loss of certain physiological functions (Ye et al. 2016; Narayanan et al. 2016). Lipid oxidation, also known as lipid peroxidation, is widely recognized as one of the most significant symptoms of oxidative stress, since it propagates free radicals through chain reactions (Ayala et al. 2014). The effects of severe lipid peroxidation can be devastating to cellular components. It is particularly vulnerable to this process when it comes to cellular membranes, which are crucial to maintaining cell integrity and function. In the course of lipid peroxidation, membranes' barrier function can collapse, resulting in their disintegration (Alché 2019). It is possible for cellular organelles to suffer profound consequences as a result of disintegration of membranes. Various cellular functions are performed by mitochondria, endoplasmic reticulum, and lysosomes. These organelles can be damaged by lipid peroxidation, impairing their function and potentially causing cellular dysfunction. Other

biomolecules within the cell can also be affected by lipid peroxidation. A lipid peroxidation-induced oxidative stress can lead to oxidative stress and alter the functional properties of proteins responsible for various cellular processes. Mutations and other abnormalities can also be caused by oxidative damage to DNA and RNA, the genetic material of the cell. Aldehydic secondary products are among the end products of lipid peroxidation. Aldehydes such as malondialdehyde, 4-hydroxy-2-nonenal, 4-hydroxy-2-hexenal, and acrolein belong to this class. In lipid peroxidation, these aldehydes signal oxidative stress, a process that can cause harm to the whole plant.

### 1.2.2 Protein Modification

Several studies have shown that ROS can oxidize any proteinogenic amino acid. As a result of this oxidation of amino acids, proteins lose their metabolic, structural, transport, and regulatory functions. Furthermore, protein oxidation can accumulate toxic protein aggregates, and in severe cases of damage, it can cause programmed cell death (PCD) (Wrzaczek et al. 2013; Qi et al. 2017; Kim 2020)). Various amino acids, such as lysine and histidine, are oxidized by the products of lipid peroxidation, such as 4-hydroxynonenal and malondialdehyde. Moller et al. (2007) examined mechanisms of oxidative damage to essential plant protein complexes, including photosystem I, D1 protein of photosystem II, ribulose-1,5-bisphosphate carboxylase/oxygenase, and superoxide dismutase (SOD) (Møller et al. 2007). With the exception of D1, the damage to these protein complexes is likely caused by singlet oxygen and requires hydroxyl radical (OH) biosynthesis catalysts that are catalytically active. Overall, ROS oxidation of amino acids can result in functional impairment of proteins, toxic aggregate formation, and in some cases, PCD. Plant protein complexes can also be oxidized by certain products of lipid peroxidation, especially when catalytically active transition metals are present. Secondary protein carbonylation occurs when aldehydes are added, which are produced during lipid peroxidation (Baxter et al. 2014; Qi et al. 2017; Huang et al. 2019). Aldehydes are usually carbonyl species with chain lengths ranging from three to nine carbon atoms. The reaction between aldehydes and proteins results in the carbonylation of the proteins, resulting in the addition of a large, reactive group. The covalent intermolecular cross-linking, cleavage, and alteration of the rate of degradation of proteins are all harmful effects of this process. Consequently, these modifications inhibit the function of proteins enzymatically and physiologically.

As a result of various plant stresses, such as salinity (Tanou et al. 2009), drought (Bartoli et al. 2004a, b), and cadmium toxicity (Romero-Puertas et al. 2002), higher levels of protein carbonylation have been observed. During these conditions, lipids can be peroxidized, which leads to aldehydes being produced and proteins being carbonated. As a result, affected proteins are unable to perform their functions, affecting various physiological processes. A buildup of carbonylated proteins may indicate oxidative stress and the detrimental effects it has on cellular function.

### 1.2.3 Damage of Carbohydrates

Through cellulose and pectin, carbohydrates provide mechanical support and shape to plant cells. They also provide storage for reduced carbon in the form of starch and sucrose (Bai et al. 2020; Hu et al. 2020). By regulating enzyme activity and osmotic pressure, low molecular weight sugars derived from carbohydrates play an important role. Furthermore, certain carbohydrates, such as flavonoids and mannitol, act as non-enzymatic antioxidants, contributing to plant resistance to oxidative stress. Carbohydrates can, however, be harmful to plants when they are oxidized (Herman et al. 2017). Carbohydrates can be damaged by oxidative processes, and this can interfere with the plant's metabolism. Despite carbohydrates' importance for plant growth and survival, their vulnerability to oxidative damage underscores the importance of understanding their role in stress responses.

The copper ion ( $\text{Cu}^{2+}$ ) can generate hydroxyl radicals ( $\bullet\text{OH}$ ), which can react non-enzymatically with xyloglucans and pectins in plant cell walls, causing their breakdown and loosening. Under normal conditions, this breakdown of cell wall components can facilitate cell expansion and promote fruit ripening. Certain developmental processes benefit from this reaction. During stressful conditions, when copper (Cu) and iron (Fe) catalytic activities increase significantly, this non-enzymatic reaction may be pathophysiological. Plant growth and physiology can be adversely affected by excessive hydroxyl radical production under stress conditions. Plant health and survival can be negatively affected by the overproduction of hydroxyl radicals caused by increased copper and iron activities, potentially due to metal stress. In other words, under normal conditions,  $\text{Cu}^{2+}$ -generated  $\bullet\text{OH}$  can have beneficial effects on plants, but when it occurs uncontrollably during stress it can affect plants negatively.

### 1.2.4 Damage to Nucleic Acids

Plants' nucleic acids, including DNA and RNA, can be damaged by oxidative stress. DNA strands can be broken by ROS directly attacking the sugar-phosphate backbone (Pourrut et al. 2011). Genetic code mutations or deletions can result from these breaks, which affect the normal functioning of the plant. Additionally, ROS can modify DNA bases (adenine, guanine, cytosine, and thymine), forming oxidized bases. During DNA replication, oxidized bases can result in mutations if not repaired correctly. It is also possible for ROS to cause oxidative damage to RNA. Sugar moieties and bases in RNA can undergo oxidative modification, impairing their stability and functionality. Damaged RNA molecules may not be properly translated into functional proteins or may interfere with cellular processes.



### 1.3 Melatonin Mediated Scavenging of ROS

It has been observed that melatonin and its byproducts exhibit significant antioxidative properties (Kumar et al. 2022a, b). In addition to combating reactive oxygen species, these byproducts are also highly effective against reactive nitrogen species (RNS). Melatonin and its byproducts protect against free radicals and oxidative stress through a variety of mechanisms, including direct neutralization of radicals and byproducts, the production of antioxidant enzymes, the suppression of enzymes that promote oxidation, and the maintenance of mitochondrial balance (Tiwari et al. 2020a, 2021a, b, 2022; Altaf et al. 2023). A single electron and hydrogen are transferred by melatonin to counteract free radical species (reference omitted). Through its direct interaction with reactive oxygen species (ROS), it improves plant resilience by neutralizing ROS (such as superoxide and hydroxyl radicals), reactive nitrogen species (such as nitric oxide and dioxide radicals, azide radicals, and peroxytrite radicals), and other oxidative agents (Reiter et al. 2016; Bian et al. 2021). Oxidative DNA damage is primarily caused by the hydroxyl radical, which is the most reactive free radical within ROS. It is also known that melatonin is better at scavenging hydroxyl radicals than mannitol and GSH. In tomatoes, melatonin can reduce superoxide and hydrogen peroxide production by reducing oxidative stress caused by nickel. In addition, it enhances Arabidopsis' high light tolerance by neutralizing hydrogen peroxide and superoxide. It has been observed that external melatonin stimulates internal melatonin synthesis, which in turn suppresses the buildup of hydrogen peroxide, superoxide, and MDA under various abiotic stress conditions (Ahammed et al. 2019; Sharafi et al. 2019). By reducing cell membrane damage and improving photosynthesis, this allows cells to function more efficiently. Furthermore, melatonin derivatives, such as AFMK and c3-OHM, have demonstrated excellent radical scavenging capacity for hydroxyl and hydroperoxyl radicals. Plants under stress are therefore protected from ROS and RNS by melatonin and its byproducts. The mechanistic insights on melatonin mediated oxidative stress mitigation have been depicted in Fig.1.1.

#### 1.3.1 Melatonin Panels Lipid Peroxidation

The role of melatonin in ameliorating lipid peroxidation has been extensively studied in diverse abiotic and biotic stresses (Wang et al. 2013; Li et al. 2016; Tiwari et al. 2020a). Under drought stress conditions it was observed that melatonin application showed priming effects in *Medicago sativa* and protected the plants from drought induced oxidative stress. Lower levels of lipid peroxidation (MDA content) as well as H<sub>2</sub>O<sub>2</sub> content were observed in melatonin primed drought stressed plants (Antoniou et al. 2017). The effects of drought stress on kiwifruit seedlings were observed to hinder biomass accumulation, damage cellular membranes, and inhibit photosynthesis. It was found, however, that seedlings were mitigated in a dose-dependent manner by melatonin irrigation. Melatonin reduced lipid peroxidation by reducing the production of reactive oxygen species (Liang et al. 2019). Drought



stress impeded the growth of soybean seedlings, while melatonin supplementation curbed the drought induced oxidative stress by escalating the activities of certain enzymes such as superoxide dismutase, peroxidase, and catalase (Cao et al. 2019). The administration of melatonin has been found to enhance the tolerance of plants to drought, potentially as a result of increased osmolyte content and heightened activities of antioxidant enzymes. These improvements help to slow down dehydration and reduce lipid peroxidation. Likewise, many examples are documented which highlight the observation of low MDA (lipid peroxidation) in drought stressed plants supplemented with melatonin in the form of foliar spray or root irrigation (Wang et al. 2013; Liu et al. 2015; Ye et al. 2016; Fleta-Soriano et al. 2017; Ma et al. 2018).

Salt stress disrupts the balance between ROS production and scavenging, resulting in an excess of ROS. Peroxidation of the lipid bilayers of cell membranes is caused by these molecules interacting with unsaturated fatty acids. By creating malondialdehyde (MDA) and other harmful by-products, cellular components are further damaged and metabolic processes are disrupted. The oxidation of lipids by ROS under salt stress can result in significant damage to cells and impaired plant growth. The effects of externally applying 0.50 mM ascorbic acid (AsA), 1  $\mu$ M melatonin, and their combination were examined on various stress responses in *Citrus aurantium* L. seedlings grown under conditions of 100 mM sodium chloride (NaCl) for a period of 30 days. NaCl is typically induced by electrolyte leakage and lipid peroxidation, which are decreased when AsA, Mel, or their combination are added to saline solution. It prevented the toxicity symptoms and pigment degradation associated with NaCl exposure (Kostopoulou et al. 2015). In wheat plants, the beneficial effects of melatonin treatment were also evident in the reduced lipid peroxidation, hydrogen peroxide content, carbonyl content, and protease activity observed in the plants under stress that received the treatment (Talaat 2021). The effects of salt stress (300 mM sodium chloride, or NaCl) and melatonin pretreatment (50, 150, and 500 mM) on leaf photosynthesis and redox balance in watermelon were examined (Li et al. 2017a). In watermelon seedling leaves, NaCl stress inhibits photosynthesis, elevates reactive oxygen species accumulation, and damages membranes. Melatonin pretreatment, however, mitigated the NaCl-induced reduction in photosynthetic rate and oxidative stress, depending on the dose of melatonin administered. Many other similar findings in diverse field and horticultural crops revealed the alleviation of salinity stress through modulation of lipid peroxidation (Altaf et al. 2020; Ke et al. 2018; Xia et al. 2017; Li et al. 2017a; Zhang et al. 2020).

A range of damaging effects can be caused by heat stress in plants, including lipid peroxidation. The polyunsaturated fatty acids within the lipid bilayers of cell membranes are attacked by ROS and related reactive species. The metabolism of plants can become unbalanced at high temperatures, resulting in an excess production of ROS. A process called lipid peroxidation occurs when these ROS interact with the lipids in the cell membranes. In addition to malondialdehyde (MDA), the breakdown products can damage the cell further. A cell membrane's structural integrity and functionality are disrupted by lipid peroxidation. As a result, membrane fluidity can be reduced, permeability can be altered, and receptors and enzymes bound to the membrane are impaired. In addition to nutrient uptake, photosynthesis,