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Recent Advances on the Pragmatic Roles of Phytomelatonin and Its Exogenous Application for Abiotic Stress Management in Plants

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Abstract

Melatonin (*N*-acetyl-5-methoxy-tryptamine), derivative of tryptophan, manifested as a conserved domain, which is ubiquitously apportioned from bacteria to higher organisms extending to fungi and algae as well. Melatonin is entailed in umpteen developmental processes of plants, including stress responses. The pleiotropic impact of melatonin in regulating transcripts of manifold genes validate its imperative contribution as multi-regulatory substance. Albeit, the progressive research regarding plants is yet prelusive in contrast to orthodox melatonin physiology in animals. This reinforces the exigency for comprehensive reassessment pertaining to its potential in biochemical and physiological processes, anti-stress response against abiotic stimulators (temperatures, salinity, drought, toxins, etc.), detoxification mechanism, and its other salubrious effect. Stressors are known to create RNS and ROS, which induces oxidative damage in plants. Cellular deterioration and mortality are a result of negligence toward oxidative damage. Tremendous quantum leap has been made in comprehending, how melatonin safeguards plants against abiotic stress. Here, focus will be on mechanistic basis of melatonin-mediated protection to abate abiotic stress. Abiotic stress induces melatonin synthesis and this redeeming upsurge in melatonin succors plant to thrive under stress conditions. Melatonin is considered an excellent antioxidant because it effectively scavenges a wide range of RNS and ROS. Melatonin maintains ROS levels in peculiar ways: (a) chemical interaction between melatonin and ROS, causing their inactivation and (b) melatonin-induced activation of SOD, POD, APX, CAT, and GPX leads to ROS detoxification. The contemporary study gives a comprehensive review on abiotic stress response of melatonin, particularly, its mitigating impact when applied exogenously in plants under environmental stress conditions. The commentary will allow the researchers to comprehend the prevailing plant stress conditions and further contemplate the tendency of phytomelatonin in crop research.

Keywords Phytomelatonin · Anti-stress · Biochemical · Physiological · Stimulators · Tryptophan

Introduction

Melatonin (*N*-acetyl-5-methoxytryptamine), a tryptophan derivative, discerned in bovine pineal gland during late 1950s was a radical discovery (Lerner et al., 1958). This is a pleiotropic molecule which is evolutionarily conserved and exists ubiquitously in fauna and flora (Hardeland et al., 2011). Melatonin is both amphiphilic and amphipathic molecules and can pass effortlessly through cell membrane to cytosol, mitochondria, and nucleus (Galano and Reiter, 2018). Melatonin occurs in numerous plant parts and is accountable for invigorating multifarious physiological process. Among plants, another major indication for diverse function of melatonin can be inferred from various species and tissue-specific differences in concentrations, ranging from very low (unnoticeable) to above 20 or 30 μg/g (Arnao & Hernández

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2020). Umpteen investigations reveal unambiguous role of melatonin in plants (Fig. 1), acting as growth regulator (Sun et al., 2021), determining growth of the explants, roots, and shoot (Mao et al., 2020), stimulate rhizogenesis (Riaz et al., 2018), and defer leaf senescence (Zhao et al., 2021). The antioxidant potential of phytomelatonin may elucidate its few physiological functions viz, to reinforce plants under abiotic stress, such as heat, drought, pesticides, UV radiations, cold, and salinity, rendering melatonin as remarkable candidate to countermeasure field crops (Bose and Howlander, 2020). Melatonin is a powerful free radical scavenger that protects against dangerous reactive oxygen and nitrogen species. Membrane receptors and nuclear receptors regulate melatonin's pleiotropic activity in living organisms (Back, 2021). Melatonin receptors also function independently, and their bioactive substance enables the replacement of reactive oxygen and nitrogen species (ROS and RNS) with melatonin (Arnao and Hernandez-Ruiz, 2019). Melatonin also plays a role in non-receptor mediated effects, such as ROS scavenging, antioxidant potential enhancement, and tissue protection from oxidative stress (Lee and Back, 2020). Eventually, the production and accumulation of ROS and RNS are rudimentary processes related to cellular and physiological pathogenesis.

Abiotic stress imparts detrimental effect on plants, limiting agricultural productivity and growth, thereby becoming a global issue. However, the proportion of agricultural lands experiencing multiple abiotic stresses is expected only to rise under changing global climate fueled by anthropogenic activities. These stresses retard plant growth and development by lowering metabolism, leading to nutrient deficiency, generating reactive oxygen species, and osmotic and ionic stress causing oxidative damage to essential components viz, proteins and lipids, and reduce root growth, enzymatic activity, water absorption, and mineral uptake efficiency (Kumar et al., 2019). Data suggest that crop productivity has severely decreased by ~ 50–82% depending upon type of stress, duration, and crop variety (Gao et al., 2007). Plants undergo numerous physiological and metabolic changes to safeguard in response to abiotic stress. Also plants are bestowed with inbuilt capacity to respond via signal transduction pathways for adjusting their metabolism (Jan et al., 2020). In order to promote sustainable agricultural practices various amendments practices have been implemented to achieve the goal (Sabkia et al., 2021).

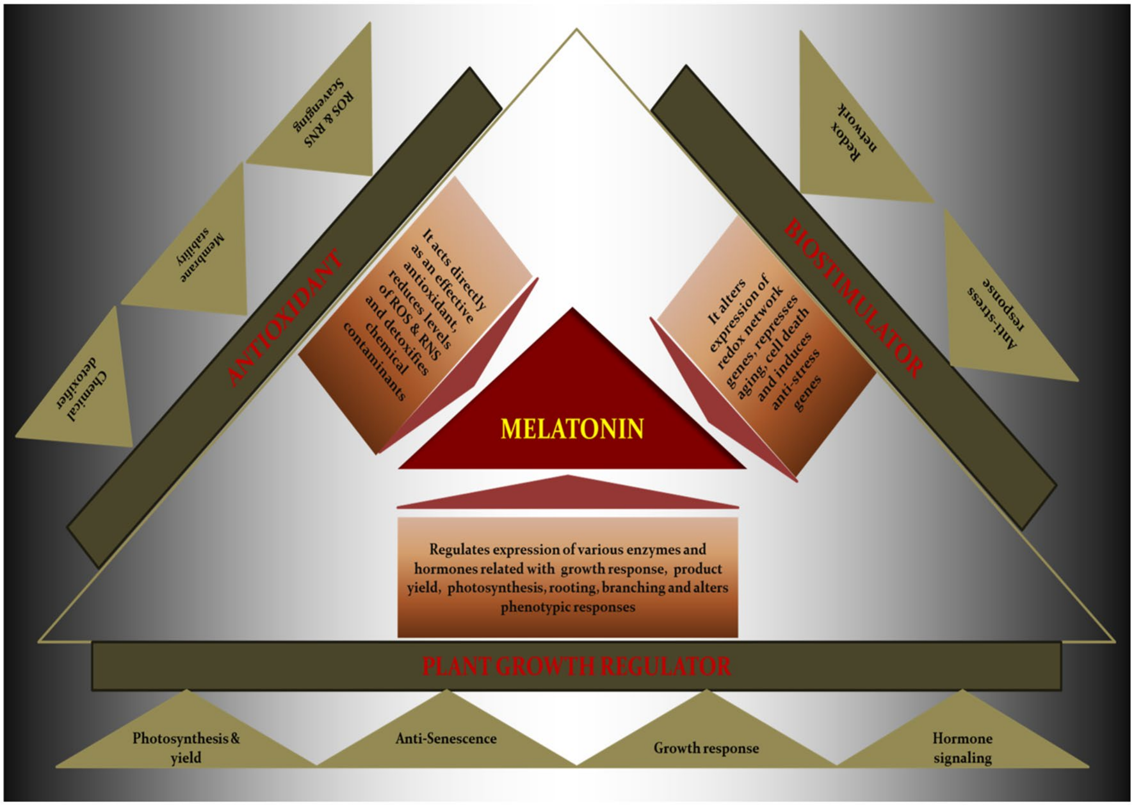

Fig. 1 Multifarious role of melatonin in various physiological processes of plant system. The figure highlights the antioxidant, biostimulant, and plant growth regulation properties of melatonin

Selection of some exogenous chemical priming can regulate plant metabolism and improve plant resistance. Integrating melatonin to agronomical practices reportedly provides numerous benefits. Mentioning particularly about melatonin priming, it has been observed to enhance photosynthesis of *Solanum lycopersicum* under low-temperature stress (Yang et al., 2018) and salt stress (Zhao et al., 2016) and it could be due to action of melatonin on redox regulation of photosynthetic electron transport and synthesis of D1 protein (Zhou et al., 2016). Seed priming with melatonin has shown improved seed germination and resilience under adverse conditions. Seed priming with melatonin is one such method used to regulate plants metabolic processes during early stages of germination under stress conditions. Seed priming is a promising method that confers uniform germination by reducing imbibitions time, activating germination inducers, repairing breaks in DNA, and regulating hydration levels (Marthandan et al., 2020). It has been documented that melatonin pre-treatment neutralized the detrimental aging effect in aged oats seeds. Primed seeds were found to have restored membrane integrity and up-regulated energy generation pathways (Yan and Mao, 2021). Melatonin-primed seeds possess higher content of osmoprotectants, up-regulation of energy-producing pathways (Jan et al., 2022), and enhanced protein content, which may lead to improve abiotic stress response in plants (Rajora et al., 2022). Various modes of melatonin priming are seed priming, leaf spray, and root application and seed priming and leaf spray are found to be work better in alleviating stress. Using melatonin to improve crop resistance and mitigate photo-inhibition is an important agricultural management measure.

Ergo, it is concluded that fundamental role of melatonin in life forms is to boost antioxidant defense system and serve as a primary respondent to stress conditions (Arnao and Hernandez-Ruiz, 2019). Promulgating the advances of melatonin in previous years, its mode of action in plants is explored extensively. The contemporary study gives a comprehensive review on abiotic stress response of melatonin, particularly, its mitigating impact when applied exogenously in plants under environmental stress conditions. The commentary will allow the researchers to comprehend the prevailing plant stress conditions and further contemplate the tendency of phytomelatonin in crop research.

Melatonin Modulates Plant's Various Attributes

Multifarious role of melatonin among higher plants have been studied thoroughly yet data for all cases is scarce (Table 1). Among various experiments executed to identify exact role of phytomelatonin, its role as promising growth regulator has been extensively reviewed. The circadian oscillator in plants is capable of regulating various biological processes, viz metabolic modulation, gene regulation and protein stability, thereby increasing growth rate and photosynthesis and further may influence seed production and flowering Arnao and Hernandez-Ruiz, 2019). The subject discussed below outlines the physiological function of phytomelatonin and protecting plant's integrity under stress conditions.

Plant Growth and Development

The tryptophan derivatives, melatonin, and IAA have alike chemical conformation and their structural homology allows them to regulate synonymous activity in plants. IAA and melatonin contain indole structure, yet differ in

Table 1 Different roles of melatonin in higher plants

Function of melatonin	Physiological response	Reference
Vegetative development	Stimulates growth of different seedlings	(Nabaei and Amooaghaie, 2019)
Vegetative development	Stimulates or prevents growth of primary roots	(Mao et al., 2020)
Vegetative development	Facilitates lateral and adventitious rooting in several species	(Hu et al., 2020)
Vegetative development	Alters the developmental pattern of branching	(Li et al., 2020a, b)
Vegetative development	Defers loss of chlorophyll during leaf-induced senescence	(Liang et al., 2018)
Vegetative development	Promotes photosynthesis, carbon dioxide assimilation, and biomass	(Zhang et al., 2019a, b)
Vegetative development	Facilitates rhizogenesis and caulogenesis in tissue culture	(Golovatskaya et al., 2020)
Vegetative development	Acts as chronoregulator	(Xu et al., 2019)
Reproductive development	Influences various stages of flowering in various species	(Arnao and Hernandez-Ruiz, 2020)
Reproductive development	Promotes fruit development and seed production in many species	(Sun et al., 2020)
Stress mitigation	Triggers plant growth under stress conditions, for example, drought, cold, herbicides, high temperature, and UV radiations	(Liu et al., 2020)
Stress mitigation	Enhances germination rate in stressed seeds	(Wu et al., 2020)
Stress mitigation	Provides resistance against various pathogens	(Chen et al., 2020)

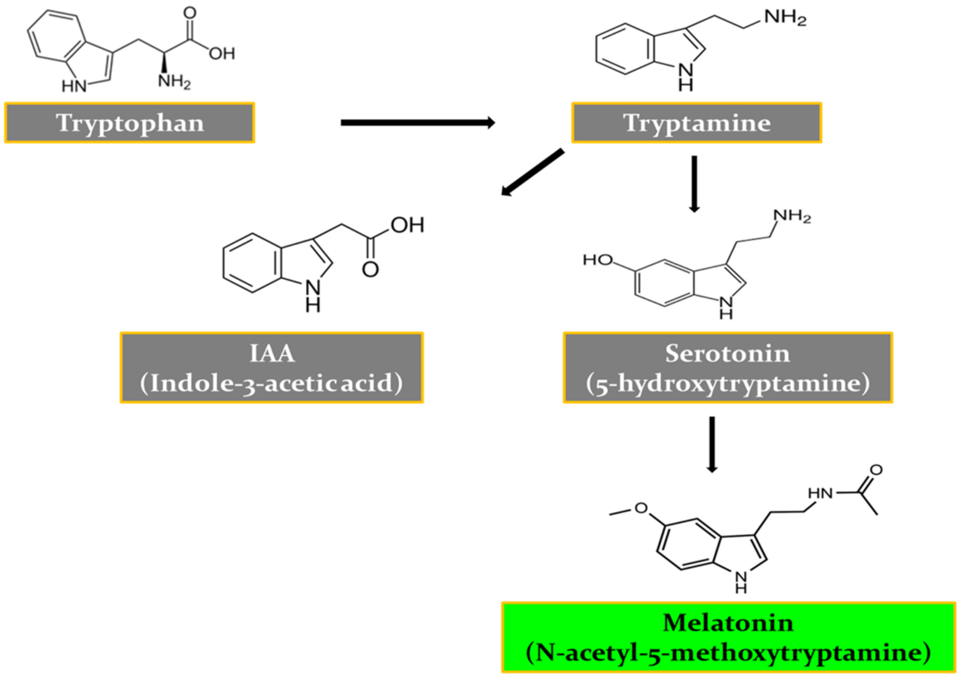

Fig. 2 An overview of biosynthetic pathway of melatonin in plant system involving tryptophan as precursor molecule

bonded functional groups (Fig. 2). Structurally, auxin and melatonin exhibit numerous similarities, for example, planar aromatic-ring, hydrophobic transition region, and carboxylic acid-binding site. While, melatonin improves different growth parameters in plants, but in majority of cases the mechanisms are partly defined (Tan and Reiter, 2020). Thereon, melatonin exhibit IAA-like activities. To give an instance, in *Arabidopsis thaliana* transcriptome data were analyzed where 16 auxin-related genes were identified and due to melatonin treatment, the expression pattern was metamorphosed. Melatonin works in correlation with auxin in order to foster secondary root growth of *Arabidopsis thaliana* (Ren et al., 2019). In woody plants, it was inferred that melatonin facilitates adventitious root development. Melatonin's involvement in IAA signaling pathway was also ascertained by RT-qPCR which suggests that melatonin induces expression of IAA biosynthesis and signal transduction-associated genes (Mao et al., 2020). Melatonin-dosed soybean cultivars produce more pods and seeds relatively to untreated one (Bawa et al., 2020). Melatonin regulates root formation in concentration-dependent manner in tomato (*Solanum lycopersicum*) (Siddiqui et al., 2020), mustard (Brassica) (Dai et al., 2020), and various monocot plants (Danilova et al., 2020). Succinctly, various studies suggests that phytomelatonin invigorates seedling growth (Mir et al., 2020), promotes or prevents primary root growth (Yang et al., 2021), facilitates adventitious and lateral root progression (Gokbayrak et al., 2020), impedes delay-induced leaf senescence by improving photosynthesis, carbon dioxide uptake, and biomass accretion (Zhao et al., 2021), and stimulates caulogenesis and rhizogenesis in organotypic culture (Golovatskaya et al., 2020).

Photosynthesis and Pigmentation

Plants perform photosynthesis by converting light energy to chemical energy and subsequently utilize converted energy for the proliferation. Plants being sessile are incessantly exposed to array of environmental stresses, causing extensive yield loss. Abiotic stresses, for example, cold, salinity, drought, heavy metal, and pesticide, result in electron transport chain (ETC) distortion, inducing photo-oxidation and thereby decreasing photosynthetic efficacy (Jan et al., 2020). Stress causes ultrastructural changes in leaf chloroplasts and mitochondria, resulting in uncontrolled generation of reactive oxygen species (ROS) (Debnath et al., 2021). The photosynthetic efficiency is determined by total chlorophyll content, and an increase in ROS produces a significant fall in chlorophyll content inside plants (Siddiqui et al., 2020). Plants with a strong root system and high photosynthetic capability benefit from melatonin pre-treatment. Melatonin supports plant development, accelerates photosynthetic carbon absorption, and aids in the protection of cellular proteins (Meng et al., 2021). Many studies were conducted to validate the active participation of melatonin in enhancing photochemical efficiency of photosystem II in plants. Melatonin treatment remarkably improved *Fv/Fm* and *PLABS* in zinc oxide stressed plants, indicating stimulatory role of melatonin on quantum yield of photosystem II and light assimilation efficiency (Zuo et al., 2017). Likewise, experimental evaluation validates the active participation of phytomelatonin in enhancing photosynthetic efficiency. In *Solanum lycopersicum* melatonin treatment (100 µM) elevated endogenous melatonin level, photosynthetic pigment content, and up-regulated gene expression of photosynthetic pigments under stress conditions. Melatonin amplified CO_2 assimilation, that is, $V_{c,max}$ (maximum rate of ribulose-1,5-bisphosphate carboxylase, Rubisco) and J_{max} (electron transport of Rubisco formation) along with increased Rubisco activity and FBPase activity. Under stress conditions melatonin increased electron transport rate (ETR), PSII efficacy (ΦPSII), and photochemical quenching co-efficient (qP). Concisely, melatonin treatment enhanced chlorophyll *a* fluorescence which in turn maximizes electron transport efficiency (Jahan et al., 2021). Stomata in leaves are the primary path for gas exchange and have a major role in photosynthesis and respiration. Implementation of melatonin improves stomatal conductance in *Vitis vinifira* and *Malus domestica* (Yang et al., 2020; He et al., 2020). Also melatonin seed treatment increases stomatal size and regulates its opening in plants during stress conditions thereby boosting stomatal conductance and capacity. In *Cucumis sativus* plants, melatonin treatment improved the photosynthetic rate, antioxidant capacity, and lowered chlorophyll degradation ultimately mitigating abiotic stress (Ali Shah et al., 2020). Findings also reveal that melatonin delays dark-induced leaf senescence and decreases ROS generation in *Vitis vinifera*. It enables scavenging of antioxidant enzymes, such as CAT, POD, and SOD. In cessation, the results also manifest that melatonin subdues translation of leaf senescence associated genes (SAGs) (Shi et al., 2019). In drought-stressed *Glycine max* seedling the transcriptome analysis unveiled the expression of photosynthetic genes up-regulated by melatonin. Distinctly, some interesting genes up-regulated by melatonin are PsaK and PsaG (subunits of photosystem I), PsbO and PsbP (proteins of photosystem II), PetF (ferredoxin gene) and VTC4 (involved in ascorbate biosynthesis) (Imran et al., 2021). In microalga *Ulva* sp. melatonin showed few additive effects on chlorophyll content (Hardeland 2019). Similar evidences were reported where melatonin imparted protective role on photosynthetic pigments in cold-stressed *Triticum* (Zhang et al., 2021), salt-stressed *Cucumis sativus* (Zhang et al., 2020), drought-stressed citrus (Jafari and Shahsavar 2020), and salt-stressed tomato (Altaf et al., 2021).

Anti-Senescence

From very long melatonin has been recognized as anti-aging component in mammals (Reiter et al., 2018). Being a potent antioxidant in living species its salubrious effects have been discussed in detail (Bose and Howlader 2020). Melatonin behaves as a signal to activate antioxidant enzymes or bolster other antioxidants in particular GSH, AsA, and polyphenols (Jahan et al., 2021). For instance, $CAND_2/PMTR_1$ maintains ROS equilibrium via modulating gene expression and activity of ROS scavenging enzymes such as CAT, POD, and SOD in Arabidopsis (Li et al., 2020a, b). Albeit, the impact of melatonin on plant sustenance remained unexamined comprehensively, yet its involvement in leaf senescence has received limelight (Zhao et al., 2021). It was promulgated that melatonin decelerated dark-induced senescence and this serendipitous effect was verified in *Actinidia deliciosa* (Liang et al., 2018). The impact of melatonin on anti-senescence contributes to its exceptional antioxidant properties. Through various examinations it is evident that melatonin regulates redox parameters viz, lowering ROS levels and rising AsA and GSH levels along with antioxidant enzymes which corresponds to its anti-senescence effect. Howbeit, studies on melatonin-induced leaf senescence fail to present a reconcilable picture. Multifarious phytohormones viz, salicylic acid, ethylene, and jasmonic acid involved in inducing or stimulating senescence were up-regulated by prodigious set of genes and this phenomenon was mediated by melatonin as conferred from whole-genome expression analysis of melatonin-treated *Arabidopsis* plant (Zia et al., 2019). Irrespective of influence of melatonin on senescence, synergy between melatonin and aforementioned phytohormones should be envisaged. To prevent leaf senescence, it is essential to preserve chlorophyll activity, ergo, role of melatonin in regulating photosynthetic activity demands preferential attention. In trailblazing study, exogenous melatonin safeguards chlorophyll from deterioration in Chinese flowering cabbage (Tan et al., 2019). Impact of melatonin in protecting chlorophyll was also studied in other cultivars, including *Solanum lycopersicum* (Yin et al., 2019) and *Oryza sativa* (Choi and Back, 2019). In transcriptome analysis, treatment of melatonin up-regulated expression of PsaK and PsaG (two subunits of photosystem I), PsbO and PsbP (two sub units of photosystem II), and ferredoxin PetF, while it down-regulated expression of chlorophyllase and PaO (Cao et al., 2019). Melatonin prevents leaf senescence by preserving chlorophyll, as evidenced by several studies. The proteome transformation that occurs during leaf senescence was studied in a groundbreaking study. Such discoveries provide a plethora of data and reveal many of the functions of melatonin in plant physiological systems. Natural senescence affected 622 proteins, but melatonin therapy altered just 309 proteins, according to climactic proteomic data. Melatonin affected many proteins involved in the senescence process during cessation, further down-regulating those proteins that are normally up-regulated during natural senescence. Furthermore, during a natural senescence event, proteins involved in photosynthesis were shown to be up-regulated (Zhao et al., 2021).

Melatonin for Abiotic stress Forbearance

Tremendous quantum leap has been made in comprehending, how melatonin safeguards plants from abiotic stress. Here, focus will be on mechanistic basis of melatonin-mediated protection to abate abiotic stress. Abiotic stress induces melatonin synthesis and this redeeming upsurge in melatonin succors plant to thrive during stress conditions.

Melatonin levels and epigenetic changes in plants during stress conditions

Melatonin perpetuates in plants under normal condition. While, melatonin concentration is relentlessly distressed by pernicious conditions, including heat, cold, UV intensity, drought, salinity, and metal stress (Sajjad et al., 2020). Melatonin concentration within cell is responsive to extraneous condition. Briefly enumerating, in *Arabidopsis thaliana* significant increase in melatonin levels under UV-B stress condition was observed which in turn provided resistance against UV-B stress (Yao et al., 2021). In melatonin synthesis pathway serotonin N-acetyltransferase (SNAT) and N-acetylserotonin methyltransferase (ASMT) are vital enzymes. The endogenous melatonin level increases by 2–threefold in *Cucumis sativus* amid salt stress conditions (Qi et al., 2020). The enzymes involved in melatonin biosynthesis are over-expressed by stress stimuli. In *Oryza sativa*, melatonin biosynthesis inflates under heat and dark conditions because of increased regulation of SNAT and ASMT (Choi and Back 2019). Hydroxyindole-*O*-methyltransferase (HIOMT; also known as ASMT) shows higher activity in *Zea mays* cotyledons under extreme salt conditions, culminating with increased melatonin levels (Ahmad et al., 2020). Various reports on mechanisms rudimentary to regulation of melatonin synthesis during stress stimuli emphasize on up-regulated transcription factors of aforementioned enzymes and isoenzymes. Over-expressing HIOMT/AANAT increases melatonin accumulation in switchgrass under salinity stress and simultaneously provides tolerance under such conditions (Huang et al., 2017). Up-regulation of *MdTDC1*, *MdASMT1, MdT5H4*, and *MdAANAT2* (genes involved in melatonin biosynthesis) regulates water balance in *Malus hupehensis* under drought conditions (Ahn et al., 2021). Melatonin endows drought resistance by improving photosynthetic efficiency and promotes accretion of proline and total soluble sugars in grafted *Carya cathayensis*. Also, metabolomic study uncovers that melatonin modulates metabolic pathways viz, carbon fixation, sugar metabolism, chlorophyll, carotenoids, and phenylpropanoid synthesis (Sharma et al., 2020). Forbye, selenium induces transcription of *TDC, SNAT, ASMT*, and *T5H* genes associated with melatonin biosynthesis in *Solanum lycopersicum*, leading to increased melatonin levels and assists in cadmium detoxification (Mathur and Pramanik 2020). External factors certainly affect the melatonin level in plant tissues. Plants raised indoor under controlled conditions possess less melatonin content comparatively to field grown plants under diverse condition. Plants cultivated in daylight have 2.5–3 times increased melatonin within roots and leaves, respectively, in comparison to plant grown under in vitro conditions (Yu et al., 2018). Similarly, in *Solanum lycopersicum* the monochromatic red and blue light change fruit quality and increase endogenous melatonin levels during fruit ripening (Li et al., 2021). The above segment divulges that melatonin partakes in stress tolerance.

Melatonin-Mediated Abiotic Stress Tolerance

The cloned gene of phytomelatonin synthesizing enzyme corroborate those plants possess indispensible enzymatic machinery for melatonin synthesis. Apart from biosynthesis, plants can imbibe exogenous melatonin to accumulate within tissues (Zhang et al., 2021). The impact of exogenous melatonin varies from being restorative to ineffective or even toxic. The concentration is an actual basis of this marginal distinction. Melatonin plays heterogeneous roles in modulating plant's development and growth under varying concentrations within plant species (Table 2) (See Fig. 3).

Drought Stress

The repercussion of drought stress is extensive crop loss, thus posing jeopardy to sustainable agriculture. Numerous studies are carried out to examine the relation between melatonin and drought stress (Sharma et al., 2020). Limited watering triggers melatonin synthesis, and melatonin application mitigates drought-induced encumbrance on root elongation and seed germination (Dai et al., 2020). It has been proven that during drought stress, melatonin enhances antioxidant enzyme activity and increases content of antioxidants viz, GSH, AsA, and phenolic compounds, consequently decreases ROS accretion and palliates oxidative damage (Xia et al., 2020). Water deficiency curbs plant growth and development attributable to decreased photosynthetic rate. Besides, protecting chlorophyll, melatonin also boosts stomatal function in association with abscisic acid, causing closure of stomata which maximizes tolerance against drought-induced stress (Wang et al. 2021a, b). It is revealed that melatonin down-regulated abscisic acid synthesizing gene, namely 9-cis-epoxycarotenoid dioxygenase 3 gene *MdNCED3*, and up-regulated its catabolic genes *MdCYP707A1* and *MdCYP707A2*, thus lowering abscisic

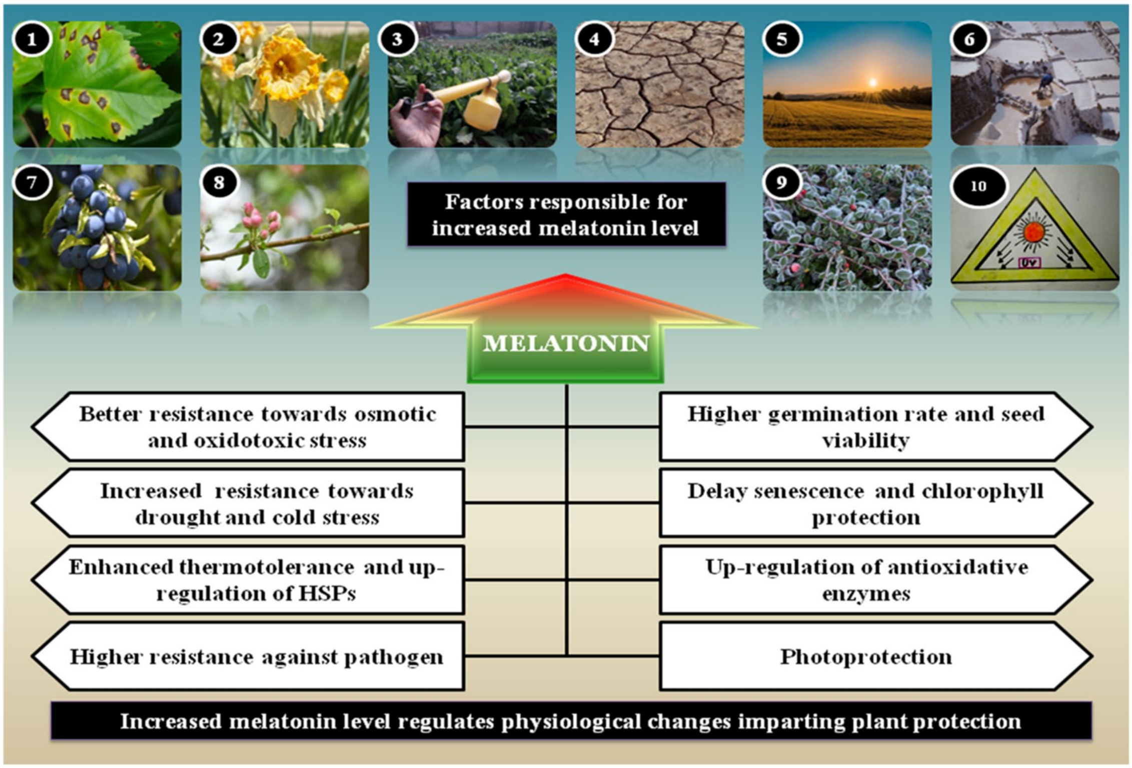

Fig. 3 Increase in Melatonin level and their corollary for plant protection and stress tolerance is presented in pictorial form. (1) Pathogen attack, (2) senescence, (3) Chemical stressors, (4) Drought, (5) Heat, (6) Salinity, (7) Developmental stage—Fruit ripening, (8) Developmental stage—Flower bud, (9) Cold, and (10) Intense UV radiation. 1 – 9 correspond to the increased melatonin content. HSPs; Heat shock proteins

acid contents and retains stomatal function during drought conditions (Ahn et al., 2021). The enhanced stomatal function acts synergistically with antioxidant network to skirmish drought stress.

Cold and Heat Stress

Ambient temperature is predominant aspect for determining momentum of plant growth. Both heat and cold stress alters redox homeostasis, leading ROS accretion and membrane impairment. Exposure to cold temperatures stimulates physiological and biochemical changes which provoke restricted growth and loss of vigor in plants. Primary site of cold-induced injuries are cell membranes. Cold stress causes alteration in cell structure and cell wall components. The defensive role of melatonin during cold stress has been studied in *Capsicum annuum*. The seeds treated with melatonin activated the antioxidant defense system and minimum disorganized cell ultra-structure was observed. In order to combat oxidative damage, melatonin up-regulated *CaAPX, CaSOD, CaCAT*, and *CaPOD* genes (Kong et al., 2020). In *Solanum lycopersicum*, melatonin regulates osmo-protective and nitro-oxidative homeostasis to reinforce tolerance against heat stress. Melatonin attenuates heat-induced stress in *Solanum lycopersicum* by maintaining redox status and regulating nitric oxide and polyamine synthesis (Jahan et al., 2019). Heat stress leads to four types of mutilation: oxidative stress sourced from ROS; loss of membrane integrity; dicarbonyl stress elicited by methylglyoxal that reacts abruptly with lipids, nucleic acids, and proteins; and cell dehydration due to water deficiency caused by osmotic stress (Pardo-Hernandez et al., 2020). Heat stress elevates endogenous melatonin levels, thus enhancing thermo-tolerance due to strong antioxidant capacity of phytomelatonin (Ahammed et al., 2019). Melatonin action against heat stress is principally regulated by heat shock proteins and factors. It is revealed that HSP90 and HSP101 (heat shock proteins) and HSFA2 and HSA32 (heat shock factors) modulate melatonin-induced thermo-tolerance in *Solanum lycopersicum* (Jahan et al., 2019).

Salt Stress

Salinity stress is another major menace for agriculture, causing huge economic loss globally. Crescent data indicate that melatonin enhances salt tolerance in many plant species including *Zea mays, Solanum lycopersicum, Oryza sativa, Triticum*, and *cucumis sativus* (Li et al., 2019a, b).

Table 2 Role of melatonin in abiotic stress tolerance in plants

Abiotic stress	Plant species	Effects of melatonin	Reference
Drought	*Cucumin sativus*	Increases germination rate and root growth	Zhang et al., 2013
Drought	*Avena nuda*	Increases enzymatic activities and MAPKs and TFs	Gao et al., 2018
Drought	*Zea mays*	Improves antioxidant defense system and photosynthesis	Huang et al., 2019
Drought	*Malus*	Increases photosynthesis and chlorophylls efficiency and reduces ROS burst	Li et al., 2015
Drought	*Zea mays*	Increases photosynthetic efficiency and antioxidative enzymes activity	Ahmad et al., 2019
Drought	*Vitis vinifera*	Improves seedling growth, photosynthesis, and osmoregulation and reduces ROS burst	Meng et al., 2014
Drought	*Glycine max*	Increases leaf area index, activity of antioxidative enzymes and PS II efficiency	Zhang et al., 2019a, b
Cold	*Arabidopsis thaliana*	Up-regulates expression of CBFs, COR15a, ZAT10, ZAT12, and CAMTA1	Bajwa et al., 2014
Cold	*Rhodiola crenulata*	Enhances cryopreservation of callus	Zhao et al., 2011
Cold	*Cucumis sativus*	Increases glutathione and ascorbic acid levels	Marta et al., 2016
Cold	*Ulmus americana*	Increases re-growth of cryopreserved seeds	Uchendu et al., 2013
Cold	*Elymus nutans*	Regulates abscisic acid and downstream cold-responsive genes	Fu et al., 2017
Cold	*Citrullus lanatus*	Increases photosynthetic rate	Li et al., 2016a, b
Cold	*Camellia sinensis*	Enhances photosynthesis capacity, redox homeostasis and antioxidant activity	Li et al., 2018
Cold	*Brassica oleracea*	Improves redox homeostasis and decreases ROS burst	Zhang et al., 2016
Heat	*Actinidia deliciosa*	Increases ascorbic acid, glutathione content, and antioxidant enzyme activity	Liang et al., 2018
Heat	*Phacelia tanacetifolia*	Improves germination	Tiryaki and Keles 2012
Heat	*Festuca arundinazea*	Reduces ROS generation, electroleakage, and lipid peroxidation and enhances activity of antioxidative enzymes	Alam et al., 2018
Heat	*Arabidopsis*	Increases thermo-tolerance	Shi et al., 2015
Heat	*Zea mays*	Enhances activity of CAT, GR, glutathione, ascorbic acid, osmoregulation system, and methylglyoxal detoxification	Li et al., 2018
Heat	*Solanum lycopersicum*	Improves efficiency of antioxidative defense system Pas metabolic pathway and ascorbic acid and glutathione cycle	Jahan et al., 2019
Salinity	*Solanum lycopersicum*	Maintains photosynthetic rate, increases quantum yield of PS II, and prevents ROS elevation	Zhou et al., 2016
Salinity	*Malus*	Increases shoot height, maintains ionic balance, and reduces ROS burst	Li et al., 2016a, b
Salinity	*Medicago sativa*	ROS scavenging and enhances antioxidant enzyme activity	Cen et al., 2020
Salinity	*Helianthus*	Increases root and hypocotyl growth and antioxidant efficiency	Mukherjee et al., 2014
Salinity	*Brassica napus*	Maintains redox and ion homeostasis and upregulates antioxidant defense genes	Zhao et al., 2018
Salinity	*Vicia faba*	Increases plant height, levels of osmolytes, phenolics, and photosynthetic pigments	Dawood et al., 2015
Heavy metal	*Brassica oleracea*	Increases germination and lowers membrane peroxidation	Posmyk et al., 2008
Heavy metal	*Solanum lycopersicum*	Increases plant biomass and photosynthetic rate and enhances phytochelatins, glutathione levels, and antioxidant defense system	Hasan et al., 2015
Heavy metal	*Citrullus lanatus*	Increases plant growth, chlorophyll content, and enzymatic activity	Nawaz et al., 2018
Heavy metal	*Triticum aestivum*	Enhances photosynthetic C assimilation, increases chlorophyll content, ATPases, and Rubisco activity	Zuo et al., 2017
Heavy metal	*Medicago sativa*	Maintains redox homeostasis	Gu et al., 2017
Heavy metal	*Nicotiana*	Increases cell culture growth and lowers ROS burst	Kobylinska and Posmyk 2016

Melatonin networking with nitric oxide regulates glutathione reductase activity and increases glutathione levels in cotyledons of *Brassica napus* during salt stress (Zhao et al., 2018). For plants under saline conditions, maintaining Na^+ and K^+ ion homeostasis turns out more difficult. Melatonin under salt-stressed conditions up-regulates *AKT1* and *NHX1* genes which are responsible for controlling ionic balance in plants (Ren et al., 2020). Exogenous melatonin rescued amassing of Cl^- and Na^+ in leaves and roots of *Oryza sativa* plants and also it increased the transcription of *OsCLC1, OsCLC2*, and *OsSOS1* in leaves and roots (Moustafa-Farag et al., 2020). Exogenous melatonin also stimulates expression of salt-inhibited genes, consequently assuaging inhibitory impact of salinity on gene expression. Genes associated with carbohydrate metabolism, ascorbate metabolism, cell division, photosynthesis, and fatty acid biosynthesis are activated by melatonin treatment in *Phaseolus vulgaris* (Elsayed et al., 2021). Melatonin treatment helps maintain Na^+ and K^+ homeostasis by triggering fatty acid β-oxidation and triacylglycerol breakdown in order to control H^+ ATPase activity of plasma membrane, thereby maintaining Na^+ and K^+ ion homeostasis in *Ipomoea batatas* (Yu et al., 2018). The signaling molecules were recently identified that acts downstream of melatonin in salt-sensitive *Oryza sativa.* These signaling molecules cause uptake of K^+ in cell during saline-stressed conditions (Yan et al 2021).

Heavy Metal Stress

Mounting level of heavy metals has constantly affected our ecosystem, arousing toxicity and stress in flora. Melatonin is well used for safeguarding plants against heavy metal stress. Seed priming with melatonin protects *Cucumis melo* from toxic copper ions. Protective role of melatonin on lateral roots has been demonstrated in copper-stressed *Cucumis melo*. Melatonin pre-treatment enhances root vigor and antioxidant activities and also decline in malondialdehyde and proline content was observed. Melatonin propelled glutathione levels, which in turn chelates excess copper ions (Hu et al., 2020). Exogenous melatonin assuages chromium stress in *Zea mays* via improving diameter, surface area, tips, and volume of roots, respectively. Melatonin assuages chromium-induced inhibition of carotenoids and chlorophyll, enhances water retention, and confers better plant growth (Malik et al., 2021). Melatonin significantly diminishes cadmium toxicity, as it reduces amassing of nitric oxide in Chinese cabbage. Also melatonin augments photosynthetic parameters and biomass under cadmium stress (Wang et al., 2021a). Improved plant performance, eventuated after melatonin treatment, along with thrust expression of melatonin-synthesizing genes, imply that manipulating phytomelatonin activity can direct toward developing highly resistant crop varieties against heavy metal toxicity (Bose and Howlader 2020). A paragon is an evaluation by Sun et al. in 2020, where exogenous melatonin induces antioxidant enzyme activity, elevates antioxidant levels, and obstructs ROS generation in *Zea mays* subjected to aluminum stress. Melatonin helps plant to re-establish redox homeostasis during heavy metal stress, by nitric oxide signaling. Melatonin offers resistance to lead and cadmium-induced oxidative damage by mediating nitric oxide cell signaling (Kaya et al., 2019). Melatonin lowers cadmium amassing by stimulating heavy metal transporter genes, such as *PCR2* and ABC transporter genes in *Arabidopsis* (He et al., 2020). In summation, all studies propose that melatonin plays a prominent role in plant acclimatization toward heavy metal stress, by serving dynamically.

Melatonin-Mediated Detoxification and Attenuation of Oxidative Stress

Melatonin production is stimulated in plants under abiotic stress. Stressors are known to create RNS and ROS, which induce oxidative damage in plants ‘crosstalk with phytohormones.’

Plants have built-in systems to resist oxidative damage in order to flourish in harsh environments. These mechanisms include an antioxidative defense system and increased antioxidant synthesis. Melatonin is considered an excellent antioxidant because it effectively scavenges a wide range of RNS and ROS (Debnath et al., 2019) (Fig. 4). Melatonin maintains ROS levels in peculiar ways: (a) chemical interaction between melatonin and ROS, causing their inactivation (Arnao and Hernandez-Ruiz, 2019) and (b) melatonin-induced activation of SOD, POD, APX, CAT, and GPX leads to ROS detoxification (Khan et al., 2020). During stress conditions plants naturally enhance their melatonin level to protect from damage. Since melatonin is a ROS scavenger and assuages oxidative damage induced by stressors in plants, concurrently, melatonin improves antioxidant capacity of organelles and regulates expression of stress-responsive genes viz, C-repeat-binding factors (CBFs) to increase plant resilience during stressed conditions (Huang et al., 2020). Mechanistic studies divulge that aforementioned response occurs at gene expression level. Melatonin controls H_2O_2 burst in plants, probably by quenching superfluous ROS and improves antioxidative enzyme activity and capacity of AsA-GSH cycle (Liang et al., 2018). Through cascade reaction, one molecule of melatonin scavenges ten ROS species, which is in contrast with typical antioxidants, as they normally detoxify one free radical per molecule (Balaji and Varadarajan, 2021). Ergo, it is inferred that rudimentary role of melatonin as potent antioxidant scavenge free radical species, including ROS and RNS (Back 2021). Exogenous melatonin reduces accretion of oxidized proteins, remits photo-oxidation damage, and increases oxidative stress-induced autophagy in *Arabidopsis* (Zhao et al., 2019). Seed treatment with melatonin assuages lipid peroxidation and electrolyte leakage caused by malondialdehyde content during plant stress response. Abiotic stresses viz, heat, cold, drought and salinity elevate the levels of ROS and MDA, which directly affects the cell membrane, causing increased electrolyte leakage in plants (Xie et al., 2020). Lately, melatonin-mediated reduction of oxidative stress was evaluated in context to phyto-toxic agents. In cassava,

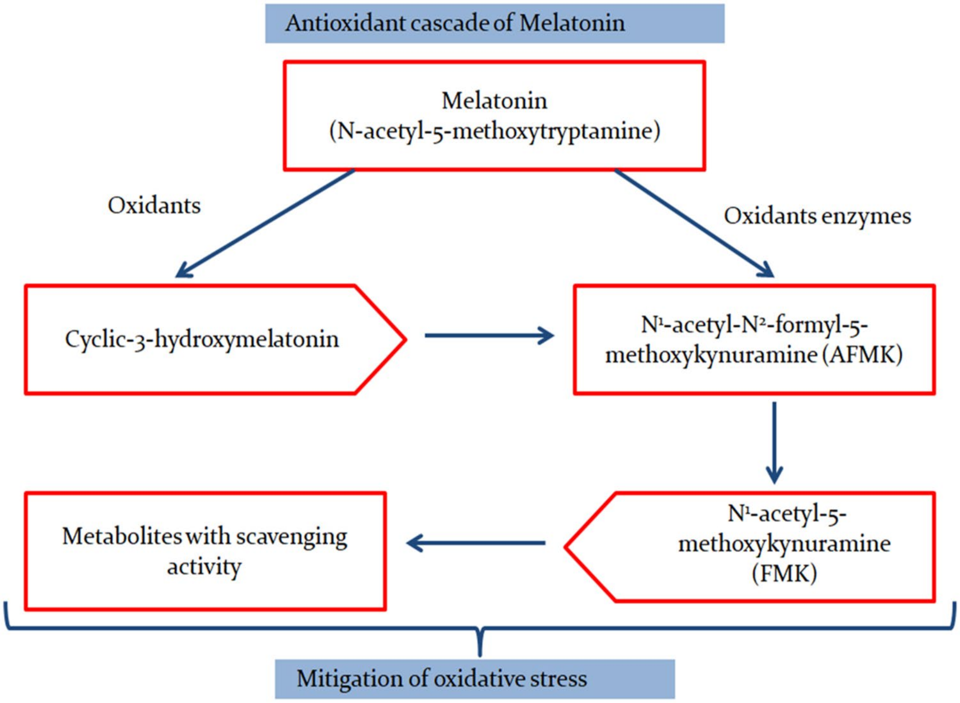

Fig. 4 Illustration of melatonin-mediated antioxidant cascade involving oxidants and oxidant enzymes to mitigate oxidative stress in plants

melatonin up-regulated ascorbate peroxidase activity and enhanced the antioxidant capacity. Howbeit, it was revealed that two enzymes (MeTDC2 and MeASMT2) involved in melatonin biosynthesis pathway show direct interaction with ascorbate peroxidase (MeAPX2). In lieu, melatonin facilitated stress tolerance and regulated redox homeostasis in cassava, which is elucidated as a survival stratagem to eradicate oxidative stress-damaged cell organelles (Bai et al., 2020). Credible evidence showed that melatonin interacts with wide array of signaling molecules including nitric oxide (NO) which generates S-nitrosylation and NO_{2-} which is regarded as prominent antioxidant-related proteins, thereby maintaining the antioxidant capacity of Asa/GSH cycle under nitro-oxidative conditions. This is a vital action to balance antioxidant potential of AsA/GSH cycle during nitro-oxidative conditions (Pardo-Hernandez et al., 2020). Also, a dynamic synchronization was discerned between melatonin and ROS, where it was seen that ROS has an ability to up-regulate melatonin biosynthesis pathway gene which leads to upsurge of endogenous melatonin content (Zhan et al., 2019). Hydrogen peroxide detoxification in plants is mediated by melatonin using glutathione which depends upon time, concentration, and plant under contemplation.

Crosstalk with Other Phytohormones

The process of plant development and growth starts at germination and pursues till senescence. Roots are requisite for carbohydrate storage, nutrient and water uptake, mechanical support, and anchoring to plants (Shen et al., 2021). Thus, root architecture holds eloquent role for plant development and growth. Auxin regulates root architecture and its significance in shaping root has been assessed. Structurally, auxin and melatonin show homology, such as hydrophobic transition region, planar aromatic rings, and carboxylic acid-binding site (Arnao & Hernández-Ruiz 2018). Besides, they share common precursor, namely tryptophan for their synthesis. On the basis of various corroborations, melatonin and auxin probably co-participate in multifarious processes related to plant development and growth, since structural similarity may hold similar roles. Also, both have powerful antioxidant potential too (Sharif et al., 2018). Melatonin works as a growth enhancer in etiolated lupin (*Lupinus albus*), behaving alike as auxin (IAA), and stimulates growth of hypocotyls at very less concentrations while imparting inhibitory effect at higher concentrations. Growth-promoting effect induced by melatonin is 63% comparative to auxin, regarded as auxinic effect (Hernandez-Ruiz and Arnao, 2008). Under the apprehension of various studies, the auxin-like activity of melatonin emerges more enigmatic than before. Melatonin down-regulates 1AA17, auxin-resistant 3, AXR3, acting as transcriptional suppressor of many auxin-inducible genes. Thus melatonin may obliquely cause up-regulation of auxin-dependent genes (Jahan et al., 2021). The findings stipulate that phytomelatonin is involved in stress responses at transcriptional as well as post-transcriptional levels. It was discerned that upsurge in intrinsic melatonin levels considerably stimulates root growth in *Hypericum perforatum* in vitro conditions, while accretion of serotonin, a melatonin precursor directs shoot formation. Likewise, melatonin actively participates in shaping root architecture indicating auxin-like roles (Arnao & Hernández-Ruiz 2018). Contemporary studies unfold that auxin and melatonin share dose-dependent relation to accelerate their activities, simultaneously modulating root development in plants. Moreover, auxin synthesizing gene transcripts viz, *YUC1, YUC2, YUC5, YUC6*, and *TAR2* are depleted upon melatonin treatment at a dose of 600 µM and further decreased auxin levels in melatonin-treated roots (Ren et al., 2019).

Cytokinins participate in cell cycle modulation and promote numerous developmental mechanisms in plants (Li et al., 2020a, b). Intrinsic cytokinin levels impede cytokinin signaling pathways in order to expedite senescence under diverse stress conditions. ARR genes in cytokinin signaling pathway is a downstream transcriptional controller. These genes modulate the communication among cytokinin and abscisic acid (Huo et al., 2020). It is contemplated that exogenous melatonin up-regulates transcripts of cytokinin synthesizing genes along with its transcriptional factors. Furthermore, melatonin and cytokinin treatment collectively alleviates dark-induced chlorophyll reduction in *Brassica rapa* leaves (Tan et al., 2019). Leaf senescence intensifies during heat stress, thereby thwarting photosynthesis and chlorophyll synthesis in leaves (Rossi et al., 2020), since cytokinin is involved in stress induced or inherent senescence. So, in order to pioneer cytokinin and melatonin interaction, specifically under heat stress an experiment was conducted on perennial grass during winter season. It was revealed that melatonin lowered leaf senescence via integrating with cytokinin and abscisic acid and also controlling their metabolic pathways (Zhang et al., 2017). Apparently, an experiment was carried out to scrutinize melatonin and abscisic acid interaction in stressed plants. Abscisic acid is altered by melatonin adjunct also exogenous melatonin begets up-regulation of abscisic acid catabolism genes that is two CYP707 monooxygenase and down-regulation of *9-cis*-epoxycarotenoid dioxygenase. Melatonin-amended plants manifested higher production of abscisic acid, thereby alleviating oxidative damage, reducing ROS and malondialdehyde level, and up-regulating antioxidants (ascorbate and glutathione) and enzymes activity (SOD, CAT, GR, and APX) (Arnao and Hernandez-Ruiz, 2021).

Salicylic acid and melatonin synthesis in plants have a common terminal precursor, namely chorismic acid, produced by shikimic acid – a condensation product of erythrose 4-phosphate from pentose phosphate pathway and phosphoenolpyruvic acid from glycolysis. Increased melatonin level secondarily transcribes iso-chorismate Synthase-1 gene, which mediates salicylic acid biosynthesis (Hernandez-Ruiz and Arnao, 2018). Neoteric work uncovered crosstalk between melatonin and salicylic acid. An evaluation ascertains the impact of melatonin and salicylic acid on antioxidants in *M. arvensis* var *piperascens* and *M.* × *piperita* under stress condition. The combinatorial application of salicylic acid and melatonin increased antioxidant activity and ROS quenching in stressed plants (Haydari et al., 2019). Analogous results were retrieved from a study where cadmium-exposed safflower plants showed noticeable decline in activity of lipoxygenase (LOX) when supplemented with melatonin and salicylic acid. Along with this H_2O_2 and MDA (malondialdehyde) contents were reduced which indicate an important role of these phytohormones in skirmishing oxidative stress. Also, melatonin and salicylic acid increase the production of ascorbate and glutathione to alleviate the metal-induced toxicity by regulating cellular redox potential. It is accorded well that glutathione and ascorbate activate the enzymes which are present in ascorbate–glutathione cycle and succor in H_2O_2 degradation. Further melatonin and salicylic acid elevated ascorbate levels and ascorbate/dehydroascorbate ratio in metal-stressed safflower plants and promote biosynthesis of non-enzymatic antioxidants to eliminate ROS produced by metals (Amjadi et al., 2021).

Gibberellic acid plays pivotal role in plants particularly during seed germination (Tuan et al., 2018). Since, melatonin augments plant growth under various physiological processes and attempts have been made to assess its probable crosstalk with gibberellic acid, an uninterrupted link was discerned between melatonin and gibberellic acid in regard to mitigate oxidative stress induced by NaCl in *Solanum lycopersicum*. Researchers proclaim that both phytohormones were effective in lowering ROS and malondialdehyde. Melatonin behaves as an antioxidant and plunges ROS generation, whereas gibberellic acid boots the activity of antioxidant system. Besides, melatonin + gibberellic acid treatment up-regulated activity of Gly I and Gly II involved in methylglyoxal detoxification system in order to detoxify methylglyoxal (a potent cytotoxin) under NaCl stress. It is observed that methylglyoxal overproduction leads to glutathione oxidation and formation of oxidized glutathione (Siddiqui et al., 2020) Overall, phytohormone synthesis, catabolism, and crosstalk between melatonin and other phytohormones are propitious for comprehending melatonin-induced mechanisms to counteract abiotic stress-mediated oxidative damage.

Conclusion and Future Aspect

Melatonin is a nascent molecule possessing pleiotropic effects with multifarious functions in plants. It is a growth stimulator and stress alleviator in plants. The cardinal role of phytomelatonin is to provide first line of defense against oxidative stress that befalls during unfavorable conditions.

Within plant cells, melatonin, ROS, and NO form an intriguing triad which maintains redox homeostasis, perhaps melatonin acting as a vital component in redox network. Ergo, impact of melatonin in redox network can be exploited as bio-stimulator to produce healthy cultivars exhibiting enhanced photosynthesis and anti-senescence genes. An interesting and contentious discovery reveals that phytomelatonin works as indispensable regulatory element for many other phytohormones. Contemporary evidences proposes that melatonin stimulates expression of numerous compounds such as receptors, enzymes and genes associated with other hormones, namely auxin, abscisic acid, salicylic acid, gibberellic acid, and ethylene and also lately identified other signaling molecules strigolactones, nitric oxide, and brassinosteroids. Melatonin interacts with other phytohormones to regulate gene expression, stabilize proteins, and induce miRNA-mediated epigenetic modifications. Furthermore, stress-response pathways are activated, including antioxidant defense systems, ROS scavenging, and osmoprotectants, as well as the recovery of leaf ultra-structure, which helps to prevent membrane oxidation and delays senescence. Endogenous melatonin, on the other hand, is incapable of shielding plants from acute harm. In light of this, exogenous melatonin has proven to be an excellent coping mechanism in extreme situations. In conclusion, further research is needed to fully understand the effects of melatonin across the plant kingdom, as well as creative approaches to improve crop production and the agricultural economy.

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