



REVIEW ARTICLE

Unlocking the potential of phyto-melatonin for sustainable agriculture and crop resilience

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Abstract

Melatonin, a naturally occurring compound derived from the amino acid tryptophan, was first discovered in animals but has recently attracted significant interest as an important signalling molecule in plants. Plant cells produce melatonin mainly within their chloroplasts and mitochondria using a series of specialised enzymes. The recent discovery of melatonin receptors in plants, combined with growing evidence of its wide-ranging effects, suggests that melatonin functions as a true plant hormone rather than just a simple metabolite. In plants, melatonin influences many essential processes including seed germination, root and shoot growth, photosynthesis, leaf aging and stress responses. One of its most remarkable abilities is its capacity to coordinate with other major plant hormones such as abscisic acid, auxins, gibberellins, salicylic acid, jasmonic acid, brassinosteroids and ethylene. This coordination allows plants to maintain an optimal balance between growing and defending themselves when faced with environmental challenges. Melatonin protects plants through two complementary pathways. It directly scavenges harmful reactive oxygen and nitrogen species using its chemically reactive structure, while simultaneously strengthening the plant's natural defence mechanisms by boosting antioxidant enzymes like superoxide dismutase, catalase and ascorbate peroxidase. When plants encounter stressful conditions including drought, salinity, temperature extremes, waterlogging, or heavy metal contamination, melatonin helps maintain stable photosynthesis, regulate water loss through stomata, preserve chlorophyll content, balance mineral absorption and prevent membrane damage. Overall, melatonin acts as a master regulator that integrates stress tolerance with normal growth processes, making it a promising candidate for developing climate-resilient crops in modern agriculture.

Keywords: abiotic stress; antioxidant defence; hormonal crosstalk; phyto-melatonin; reactive oxygen species

Introduction

Environmental changes have increased abiotic stresses that greatly limit by plant growth and productivity. Because plants are sessile organisms, they rely on complex mechanisms controlled by plant hormones like abscisic acid, ethylene, gibberellins, jasmonic acid, salicylic acid, auxin, strigolactones, brassinosteroids and cytokinins to manage stress tolerance and development. Besides these traditional hormones, melatonin has become a significant signalling molecule in plant stress management (1). Melatonin is naturally occurring indoleamine synthesized from tryptophan. Melatonin was first identified in the bovine pineal gland of cow in 1958 by Aaron B. Lerner and his associates. According to evolutionary data, melatonin originated some 2.5 to 3.5 billion years ago in primitive forms of bacteria (2). The biosynthetic pathway of melatonin was incorporated into chloroplasts and mitochondria during endosymbiosis in eukaryotes. Melatonin's discovery in plants in 1995

has ushered in a new era in plant physiology and the plant source of melatonin is referred to as phyto-melatonin. Melatonin synthesis in plants is catalysed by enzymes like tryptophan decarboxylase (TDC), tryptamine 5-hydroxylase (T5H), serotonin N-acetyltransferase (SNAT), N-acetylserotonin methyltransferase (ASMT) and caffeic acid O-methyltransferase (COMT). Photosynthetic and respiratory activities result in the formation of reactive intermediates that require immediate neutralisation. This occurs due to the capacity of chloroplasts and mitochondria to produce melatonin (3, 4). Phyto-melatonin controls growth, rooting, photosynthesis, germination and senescence. Evidence for the involvement of the PMTR1 receptor in *Arabidopsis thaliana* supports melatonin's designation as a plant hormone. Melatonin is also an efficient antioxidant that scavenges reactive oxygen species (ROS) and reactive nitrogen species (RNS) by initiating a cascade reaction of free radicals. Under abiotic stress, endogenous melatonin concentrations rise, stimulating the antioxidant defence system in

plants and promoting stress adaptation (5). This article appraises the biochemical mechanisms that underlie abiotic stress tolerance mediated by melatonin, including antioxidation properties, hormone interactions and signalling integration.

Methodology and literature

This review was conducted following the preferred reporting items for systematic reviews and meta-analyses (PRISMA 2020) guidelines. Literature was systematically searched, screened and selected according to the PRISMA 2020 framework. The articles in the databases (Scopus, Web of Science, PubMed and ScienceDirect) were up to articles published between January 2010 and March 2025 were retrieved. Some of the combinations of the keywords that were used in search are melatonin, phytemelatonin, plant stress, abiotic stress, antioxidant, ROS scavenging, hormonal regulation, plant growth, chloroplast, mitochondria and signal transduction. Only English-language research articles and review papers focusing on melatonin in plant systems were included. Studies conducted exclusively in animals or humans, as well as publications not directly related to the role of melatonin in plants, were excluded unless they provided essential information on the evolution, biosynthesis, or signalling mechanisms relevant to phytemelatonin. The literature was limited to studies that dealt with melatonin in plants, unless pertinent to the transfer of metabolites or signalling molecules within plant systems. The duplicates were eliminated and the titles and abstracts were screened with relevance assessment, then the full-text scrutiny. A total of 1245 records were identified, of which 255 studies met the inclusion criteria and were then synthesised according to the qualitative methodology. The strategy for collecting the appropriate article was listed in Table 1.

Biosynthesis of melatonin in plants

Melatonin (N-acetyl-5-methoxytryptamine) is a biologically active indoleamine derived from tryptophan. Its indole ring structure and amphiphilic nature enable it to readily cross biological membranes and interact with a wide range of reactive oxygen and nitrogen species, contributing to its potent antioxidant activity (6). This substitution pattern places melatonin within the indolamine class, a group of compounds sharing tryptophan as their common biosynthetic precursor across both plant and animal kingdoms. The resonance stabilisation inherent to the indole nucleus confers considerable chemical durability while enabling productive interactions with a broad range of biological targets and reactive molecules (7). One of the most notable physicochemical properties of melatonin is its amphiphilic nature, resulting from the coexistence of hydrophilic and hydrophobic domains within a single molecule. This property enables melatonin to rapidly cross biological

membranes and accumulate in key organelles, particularly chloroplasts and mitochondria, which are the principal intracellular sources of ROS in plant cells. Within the molecule, the indole ring serves as the primary site for radical and electrophile quenching, while the methoxy and acetamide functional groups further enhance antioxidant potency and capacity for selective molecular recognition (8).

Melatonin exerts strong antioxidant activity through both direct and indirect mechanisms. Via direct action, it detoxifies a wide spectrum of ROS and RNS including hydroxyl radicals, hydrogen peroxide, singlet oxygen and peroxynitrite, primarily through electron donation and hydrogen atom transfer reactions. A distinguishing feature that sets melatonin apart from most conventional antioxidants is that its oxidative metabolites retain radical-scavenging capacity, thereby establishing a sequential detoxification cascade in which successive breakdown products continue to neutralise reactive species. This chain-like mechanism allows a single melatonin molecule to effectively quench multiple oxidants in succession (9), substantially amplifying its overall cytoprotective efficiency under conditions of intense oxidative stress. In plants, melatonin biosynthesis is considerably more intricate than in animals and is strongly modulated by environmental factors such as light intensity and various stress stimuli (10). The process predominantly occurs in chloroplasts and mitochondria, though several intermediate enzymatic steps are carried out in the cytoplasm and endoplasmic reticulum (ER). The pathway is initiated from tryptophan, which undergoes sequential enzymatic transformations through a series of intermediates tryptamine, serotonin, N-acetylserotonin and 5-methoxytryptamine before culminating in melatonin production (11). These biosynthetic intermediates are not confined to a single location but are distributed across multiple subcellular compartments, including the cytoplasm, Endoplasmic reticulum, chloroplasts and mitochondria (12).

The pathway proceeds in a stepwise manner across these compartments. First, tryptophan decarboxylase (TDC) acts on tryptophan in the cytoplasm, generating tryptamine. This product is subsequently hydroxylated to serotonin by tryptamine 5-hydroxylase (T5H), an enzyme anchored in the Endoplasmic reticulum membrane. Serotonin then undergoes N-acetylation to yield N-acetylserotonin, a reaction catalysed by serotonin N-acetyltransferase (SNAT), which operates within chloroplasts and mitochondria. The final methylation step, converting N-acetylserotonin to melatonin, is carried out by N-acetylserotonin methyltransferase, active in both chloroplasts and the cytoplasm (13). Notably, N-acetylserotonin produced within chloroplasts can be exported to interact with cytosolic ASMT to complete melatonin

Table 1. Strategy for collecting appropriate articles

Search strategy	Search string (Boolean search)	Web of Science	Science Direct
Plant stress	("melatonin" OR "phytemelatonin") AND ("plant stress" OR "abiotic stress")	1020	980
Antioxidant defence	("melatonin" OR "phytemelatonin") AND ("antioxidant" OR "ROS scavenging")	410	890
Melatonin biosynthesis	("melatonin" OR "phytemelatonin") AND biosynthesis AND plants	210	120
Plant growth regulation	("melatonin" OR "phytemelatonin") AND ("plant growth" OR "growth regulation")	300	150
Abiotic stress tolerance	("melatonin" OR "phytemelatonin") AND ("abiotic stress tolerance" OR drought OR salinity OR heat OR cold)	560	250
Hormone interaction and signalling	("melatonin" OR "phytemelatonin") AND ("hormone interaction" OR "signal transduction")	240	115

synthesis, while an alternative route involves 5-methoxytryptamine generated in the cytoplasm being transported into chloroplasts, where SNAT catalyses its acetylation to yield melatonin (14). The overall biosynthetic pathway in plants is illustrated schematically in Fig. 1.

Beyond this primary route, caffeic acid O-methyltransferase (COMT), a multifunctional enzyme with broad substrate specificity, contributes to melatonin production through an alternative pathway identified in several plant species, where it catalyses the methylation of N-acetylserotonin directly into melatonin. Additionally, COMT is capable of converting serotonin into 5-methoxytryptamine, which is then acetylated by SNAT to produce melatonin, offering metabolic flexibility and redundancy that may be particularly advantageous under adverse environmental conditions (15).

Occurrence of melatonin in plants

Melatonin, referred to as phytomelatonin in plant biology, is now established as a ubiquitous metabolite distributed throughout the plant kingdom, spanning algae, bryophytes, gymnosperms and angiosperms. Its concentration varies considerably across species, organs, developmental stages and prevailing environmental conditions. Reported levels generally range from trace quantities up to 20–30 $\mu\text{g g}^{-1}$, though certain species may accumulate concentrations approaching 200 $\mu\text{g g}^{-1}$ (16). Phytomelatonin has been documented across numerous plant families, with Lamiaceae, Fabaceae, Poaceae, Rosaceae and Solanaceae among the most frequently represented. Economically significant genera such as *Solanum*, *Oryza*, *Arabidopsis*, *Malus*, *Brassica* and *Prunus* have received the greatest research attention in this context.

Melatonin distribution within plants follows a distinctly organ specific - pattern. Reproductive structures including flowers, fruits and seeds tend to harbour the highest concentrations, often surpassing levels recorded in vertebrate tissues by one to two orders of magnitude. Oil and protein rich seeds such as walnut, mustard, fenugreek and sunflower frequently accumulate melatonin in the $\mu\text{g g}^{-1}$ range. Elevated concentrations in these tissues are thought to safeguard storage reserves and genetic material during seed development, dormancy periods and exposure to environmental stressors including ultraviolet radiation (17). Photosynthetic tissues, particularly leaves, typically exhibit intermediate concentrations, attributable to their high chloroplast and mitochondrial density, where melatonin actively participates in antioxidant defence and redox homeostasis. Roots, stems and certain fruits generally maintain comparatively lower yet physiologically relevant levels. Notably, a previous study identified apical to basal melatonin gradients in lupin and barley, with peak concentrations detected in actively dividing root and hypocotyl zones, pointing to a functional role in growth regulation and auxin-related signalling (18).

Melatonin accumulation is further governed by both developmental transitions and environmental inputs. Concentrations commonly peak during seed germination, early seedling establishment, flowering, fruit development and senescence (19). Abiotic factors such as temperature fluctuations, light intensity and UV radiation substantially influence biosynthetic activity, giving rise to marked variation even among individuals of the same species (15). The occurrence of melatonin across various plant species and organs is summarised in Table 2.

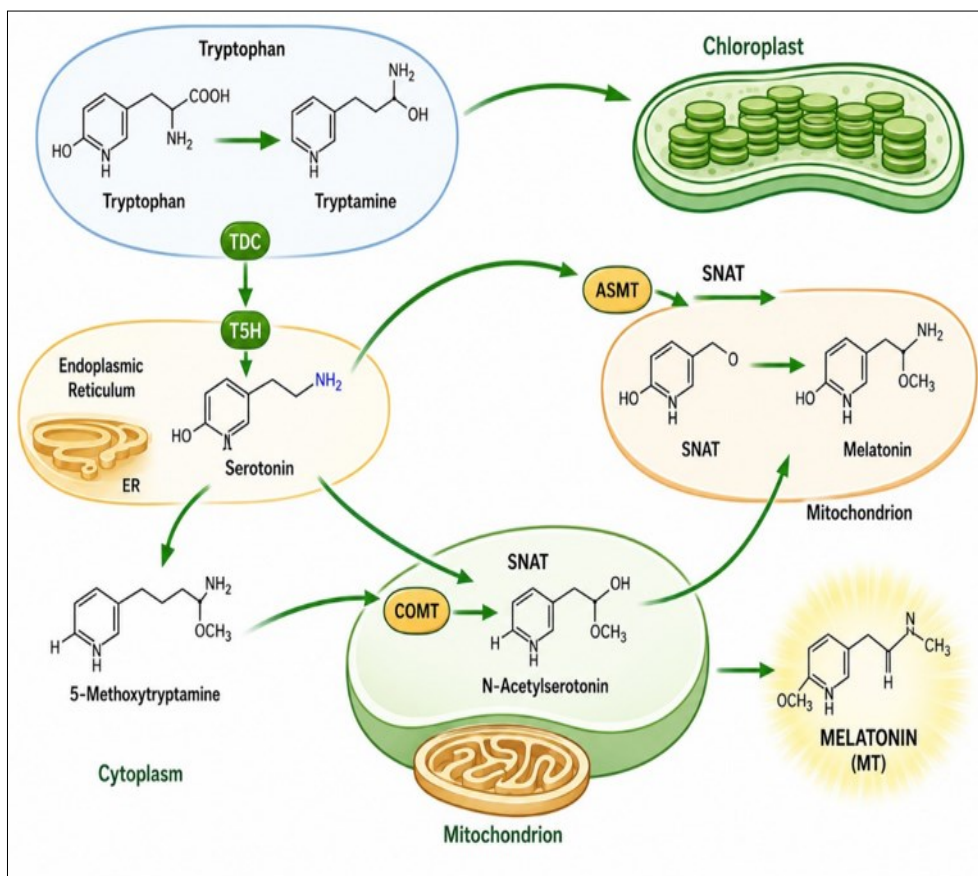


Fig. 1. Biosynthesis of melatonin in plant system.

TDC: tryptophan decarboxylase; T5H: tryptamine 5-hydroxylase; SNAT: serotonin-N-acetyltransferase; ASMT: N-acetylserotonin methyltransferase; COMT: caffeic acid O-methyltransferase.

Although numerous studies have demonstrated the beneficial effects of phyto-melatonin on plant growth, development and stress tolerance, its efficacy is not universal. The physiological responses to exogenous melatonin are often species-specific and influenced by plant genotype, developmental stage, environmental conditions and stress severity. Moreover, the effects of melatonin are dose dependent, with low or moderate concentrations generally promoting growth and antioxidant defence, whereas excessive concentrations may inhibit growth or produce negligible effects. Several studies have also reported inconsistent or limited responses under particular experimental conditions, indicating that the effectiveness of phyto-melatonin depends on multiple biological and environmental factors. Therefore, optimising melatonin concentration and application methods for individual crop species remains an important area for future research.

Interaction of melatonin with other phytohormones

Melatonin engages in extensive crosstalk with major phytohormones including abscisic acid (ABA), indole-3-acetic acid (IAA), gibberellic acid (GA) and ethylene collectively managing plant growth, development, senescence and adaptive responses to stress. Among these hormonal interactions, the melatonin ABA axis constitutes one of the most critical regulatory networks governing the balance between growth promotion and stress tolerance. In key physiological processes such as stomatal regulation, seed germination and leaf senescence, melatonin and ABA frequently act in opposition to one another (31). Exogenous melatonin application has been reported to counteract ABA-driven senescence in mature melon leaves, simultaneously preserving the structural integrity and functional efficiency of photosystem II (32). Under ABA-mediated stress, melatonin treatment upregulated expression of the respiratory burst oxidase homolog D gene (*CmRBOHD*) and facilitated controlled hydrogen peroxide accumulation, implicating melatonin in ROS-dependent signalling cascades. Beyond direct radical scavenging, melatonin attenuates ABA-induced responses

such as stomatal closure by neutralising excess ROS that would otherwise amplify ABA signalling. Although both hormones activate mitogen-activated protein kinase (MAPK) cascades, they engage distinct downstream components and phosphorylation targets, ultimately driving divergent transcriptional outcomes (33). At the gene expression level, ABA induces abscisic acid-responsive element (ABRE)-binding transcription factors and senescence-associated regulators, whereas melatonin suppresses these ABA-responsive elements, redirecting cellular activity toward growth and protection (34). Furthermore, ABA exerts a negative regulatory influence over endogenous melatonin production by downregulating key biosynthetic enzymes, notably tryptamine 5-hydroxylase (T5H) and N-acetylserotonin O-methyltransferase (ASMT). This reciprocal inhibition has led to the characterisation of the ABA melatonin interaction as a finely tuned "brake and accelerator" system that dynamically adjusts plant stress adaptation and growth trajectories (35). Melatonin also engages substantially with IAA signalling networks. Investigations in *A. thaliana* revealed that melatonin downregulates cytokinin signalling components including AHK4, AHP and ARR15 thereby modulating cytokinin-dependent root architecture and taproot elongation (36). These findings indicate that the functional parallels observed between melatonin and IAA stem from coordinated hormonal network regulation rather than any direct substitution of one hormone for another. With respect to gibberellin signalling, melatonin plays a facilitative role under stress conditions. In cucumber seeds subjected to salinity stress, exogenous melatonin application elevated the transcript abundance of GA biosynthetic genes *CsGA20ox* and *CsGA3ox* leading to increased endogenous gibberellin accumulation and enhanced germination capacity. Melatonin additionally promoted the formation of biologically active hydroxylated gibberellin forms and mitigated the inhibitory effects of sodium chloride on germination (37). This interaction encompasses coordinated regulation of GA biosynthesis, transport and signal transduction, collectively

Table 2. Occurrence of melatonin in various plant species

Family	Species / Common Name	Organ / Tissue	Melatonin content range	References
Apiaceae	<i>Daucus carota</i> L. (carrot)	Root	55.3 µg/g DW	(18)
Vitaceae	<i>Vitis vinifera</i> L. (grape)	Leaves and berries	600–3000 ng/g FW	
		Berry / skin	596–1800 ng/g FW	(20)
Poaceae (graminae)	<i>Oryza sativa</i> L. (rice)	Seed and Leaf	100–1000 ng/g FW	(5)
Solanaceae	<i>Solanum lycopersicum</i> L. (tomato)	Fruit	75–250 ng/g DW	(21)
	<i>Lycium barbarum</i> Lam. (goji berry)	Fruit / berry	530–103000 µg/g DW	(22)
Rosaceae	<i>Prunus avium</i> L. / <i>Prunus cerasus</i> L. (cherry)	Fruit	14–15050 ng/g FW	
Fabaceae	<i>Medicago sativa</i> L. (alfalfa)	Seed	16 µg/g DW	(23)
Brassicaceae	<i>Brassica oleracea</i> L. (cabbage)	Leaves and seeds	100–657 µg/g DW	(17)
Brassicaceae	<i>Brassica rapa</i> L. (Chinese cabbage)	Leaf / seed	100–485 µg/g DW	
Lamiaceae	<i>Salvia officinalis</i> L. (sage)	Leaves	280–400 ng/g FW	(19)
Rosaceae	<i>Malus domestica</i> (Suckow) Borkh. (apple)	Fruit and seed	0.05, 0.16 µg/g DW	(24)
Zingiberaceae	<i>Zingiber officinale</i> Roscoe (ginger)	Seed	3.2–120000 µg/g DW	(15)
Juglandaceae	<i>Juglans regia</i> L. (walnut)	Kernel / seed	1.2–3.5 µg/g DW	(25)
Hypericaceae	<i>Hypericum perforatum</i> L.	Leaf / flower	1823–4000 ng/g FW	(26)
Apiaceae	<i>Foeniculum vulgare</i> Mill. (fennel)	Seed	Up to 29000 µg/g DW	
Fabaceae	<i>Glycine max</i> L. (soybean)	Seed	0.059–1.833 ng/g DW (31-fold enhancement)	(27)
Moraceae	<i>Morus spp.</i> (mulberry)	Leaf (juvenile)	High (tips > mature; µg/g range)	(28)
Solanaceae	<i>Capsicum annuum</i> L. (pepper)	Seedling / fruit	High in seedlings; decreases with age	(29)
Fabaceae	<i>Phaseolus vulgaris</i> L. (kidney bean)	Sprout	529 ng/g FW	(30)

reinforcing plant performance under unfavourable growing conditions. Finally, melatonin exerts regulatory control over ethylene-mediated developmental processes, with particular relevance to fruit ripening and postharvest quality. In pear fruits, melatonin treatment markedly suppressed ethylene synthesis, decelerated peel coloration, sustained chlorophyll levels and reduced the decline in titratable acidity. Collectively, these effects demonstrate that melatonin modulates fruit maturation, nutrient metabolism and stress resilience through targeted regulation of ethylene biosynthesis and its associated signalling machinery (38). Besides its interactions with classical phytohormones, phytemelatonin also exhibits functional crosstalk with other plant signalling molecules, including salicylic acid (SA), jasmonates (JA), brassinosteroids (BRs) and nitric oxide (NO). Similar to SA and JA, melatonin enhances plant defence against biotic and abiotic stresses; however, melatonin has a broader role in integrating antioxidant defence, growth regulation and stress adaptation (39). Unlike BRs, which primarily promote cell expansion and development, melatonin provides additional protection by maintaining cellular redox homeostasis and reducing oxidative damage. It also interacts synergistically with NO to regulate stomatal movement, antioxidant enzyme activity and stress-responsive signalling pathways. Nevertheless, the effectiveness of phytemelatonin depends on plant species, developmental stage, environmental conditions and application concentration (40). Therefore, phytemelatonin should be considered a complementary signalling molecule that functions alongside other phytohormones and biostimulants to enhance plant growth and stress tolerance.

Melatonin in regulating plant growth and physiology

Regulation of seed germination

Seed germination represents a pivotal phase in the plant life cycle, encompassing a series of coordinated metabolic, cellular and molecular events essential for successful crop establishment under dynamically changing environmental conditions (41). This developmental window is characterised by extensive physiological reorganisation and mobilisation of stored reserves, rendering seeds particularly vulnerable to abiotic stressors including salinity, drought, temperature extremes and heavy metal toxicity. Such stresses disrupt endogenous hormonal equilibrium and trigger oxidative damage, ultimately compromising germination success and early seedling establishment (42). Accumulating evidence has positioned melatonin as a key signalling molecule capable of improving germination efficiency, promoting uniform seedling emergence and strengthening early seedling vigour. These beneficial effects are primarily mediated through the modulation of ABA and GA crosstalk, attenuation of ROS accumulation and upregulation of hydrolytic enzyme activities (43). At the mechanistic level, melatonin facilitates germination by dampening ABA biosynthesis or its downstream signalling while concurrently activating GA biosynthetic pathways, thereby shifting the hormonal balance in favour of germination.

Evidence from multiple species supports this hormonal regulatory model. In melon (*Cucumis melo* L.), melatonin application elevated transcript levels of GA biosynthetic genes (*CsGA20ox* and *CsGA3ox*) alongside ABA catabolic genes (*CsCYP707A1* and *CsCYP707A2*), accelerating radicle emergence under salinity-induced stress (44). Comparable outcomes were documented in cotton (*Gossypium hirsutum* L.), where melatonin restored the GA-ABA equilibrium disrupted by heat stress, thereby alleviating germination inhibition (42). Under chilling conditions, melatonin suppressed ABI5

-mediated ABA signalling in *A. thaliana*, ensuring timely progression through germination even at low temperatures (45). In addition to hormonal modulation, melatonin substantially reinforces antioxidant defence mechanisms during germination. In heat-stressed cotton seedlings (40 °C), melatonin priming elevated the activities of superoxide dismutase, catalase and peroxidase, reduced membrane lipid peroxidation and improved overall germination rates by approximately 35 % (46). Under chilling stress (10 °C) in maize, application of 25 µM melatonin raised the germination index by 4 %, an effect attributable to enhanced antioxidant capacity coupled with gibberellin-associated signalling activation. In wheat and maize subjected to polyethylene glycol-induced drought stress, melatonin-treated seeds exhibited elevated α -amylase activity and greater soluble sugar accumulation, translating into 28–45 % higher germination rates compared to untreated controls. In sorghum, priming with 50 µM melatonin synchronised germination under osmotic stress by lowering ABA concentrations and stimulating proline accumulation as an osmoprotective response.

Melatonin also demonstrates protective efficacy against heavy metal-induced germination impairment. In wheat seeds exposed to chromium toxicity, melatonin application improved germination performance and facilitated the mobilisation of stored reserves (47). Likewise, in cadmium-stressed rapeseed, melatonin priming enhanced peroxidase activity, maintained ionic homeostasis and resulted in a 32 % improvement in germination efficiency relative to stressed controls (48). Collectively, these findings highlight melatonin as a multifunctional regulator of seed germination, operating through integrated hormonal, antioxidant and enzymatic mechanisms across a broad range of stress scenarios.

Shoot and root development

Melatonin counteracts this inhibition by inducing apoplastic acidification and upregulating the expression of wall-loosening enzyme genes, thereby sustaining cell expansion even under stress. These effects are mediated both through the direct regulation of cell wall remodelling and through auxin IAA-mediated signalling pathways, as melatonin modulates auxin biosynthesis, transport and signalling to promote root growth and cell elongation. As an indoleamine compound, melatonin plays a significant role in driving cell elongation and coordinated seedling development, ultimately contributing to greater biomass accumulation, improved nutrient uptake efficiency and elevated stress tolerance (49). Under water deficit conditions, elevated ABA accumulation triggers apoplastic alkalisation, which impairs the activity of cell wall-loosening proteins such as expansins and xyloglucan endotransglucosylase/hydrolases (XTHs), consequently restricting cell expansion (50). Melatonin counteracts this inhibition by inducing apoplastic acidification and upregulating the expression of cell wall-loosening genes, including expansins (*EXPA1*, *EXPA8*) and xyloglucan endotransglucosylase/hydrolases (*XTH5*, *XTH22*), thereby sustaining cell expansion under stress conditions. Multiple studies have demonstrated the growth-promoting influence of melatonin on both shoot and root systems under adverse conditions. Previous researchers reported that combined melatonin and nitrogen application markedly improved shoot biomass in maize seedlings. Under salinity stress, melatonin facilitated peroxidase-mediated cell wall modification in maize shoots, yielding approximately 35 % greater fresh biomass accumulation relative to untreated plants. In salt-stressed maize, treatment with 100 µM melatonin increased root length, root surface area and root volume by 42 %, 38 % and

51 %, respectively, effects that were associated with elevated endogenous IAA levels and enhanced adventitious root initiation (51).

Melatonin further improves root morphology and osmotic regulation across diverse crop species. In wheat, melatonin priming augmented root length, volume and surface area, collectively supporting improved seedling establishment and early growth (52). Under stress conditions, exogenous melatonin stimulates the accumulation of compatible solutes including soluble sugars and proteins that contribute to osmotic balance and maintenance of cellular turgor. In cotton, melatonin-driven osmolyte accumulation strengthened dehydration tolerance and sustained growth continuity under stressful environments (53).

Gas exchange and photosynthetic efficiency

Abiotic stresses severely compromise photosynthesis, one of the most fundamental physiological processes in green plants. Stress conditions including drought, salinity and heat impair chloroplast integrity, disrupt photochemical reactions and reduce the generation of ATP and NADPH, collectively weakening rubisco activity and limiting carbon fixation (54). These effects are further compounded by restricted CO₂ diffusion and diminished substrate availability, which together suppress overall photosynthetic efficiency under stress. Melatonin plays a multifaceted protective role in maintaining photosynthetic performance under abiotic stress. It enhances gas exchange parameters, stabilises chlorophyll content, modulates ABA-mediated stomatal behaviour and safeguards photosystem II (PSII) efficiency through regulation of thylakoid protein turnover. Through these coordinated actions, melatonin enables crops such as wheat, tomato and rose to maintain higher net photosynthetic rates, improved intrinsic water-use efficiency (WUEi) and effective photoprotection under abiotic stress conditions. However, the magnitude of these responses varies depending on the plant species, genotype, stress severity and experimental condition (55).

Chlorophyll degradation represents one of the most consequential outcomes of abiotic stress. Environmental stress activates hydrolytic and oxidative enzymes including chlorophyllase, pheophytinase and peroxidases that accelerate pigment breakdown and diminish light-harvesting capacity (56). Melatonin effectively mitigates this damage by stabilising chlorophyll content and preserving chloroplast ultrastructure. In wheat under 20 % polyethylene glycol (PEG)-induced osmotic stress, application of 25 µM melatonin raised total chlorophyll content by 20–30 %, restored thylakoid membrane integrity and improved light absorption at 680 nm. These gains were accompanied by normalised OJIP fluorescence kinetics, reflecting reduced donor- and acceptor-side constraints on PSII activity (57). Further evidence highlights melatonin's capacity to regulate gene networks governing chlorophyll metabolism and photosynthetic machinery. In *Agrostis stolonifera* L., melatonin suppressed the expression of chlorophyll degradation-associated genes including *Chlase*, *PPH* and *Chl-PRX* (41). It also shielded chloroplast architecture from oxidative injury and supported the recovery of accessory pigments carotenoids, chlorophyll b, xanthophylls and anthocyanins under stress conditions (58). In bermudagrass, melatonin bolstered photosynthetic capacity by preventing pigment degradation and upregulating light-harvesting complex proteins (LHCA) alongside photosystem I (PSI) components (PsaG) during oxidative stress (50).

Melatonin additionally contributes to photosynthetic regulation through its influence on stomatal behaviour. Stomata serve as critical gatekeepers of transpiration, water balance and gaseous exchange. Rather than acting directly on guard cells, melatonin modulates stomatal aperture indirectly by regulating ABA homeostasis enhancing ABA catabolism while suppressing its biosynthesis, thereby lowering endogenous ABA accumulation and hydrogen peroxide levels in guard cells, both of which serve as key triggers for stomatal closure (59). As a consequence, melatonin promotes stomatal opening, sustains transpirational flow and maintains favorable leaf water status under moderate stress. This regulatory influence of melatonin on stomatal conductance and transpiration has been documented across several economically important crops, including tomato (60), rice (61) and pepper (62).

Melatonin as a master antioxidant and reactive oxygen species scavenger

Climate change-associated abiotic stresses expose crop plants to severe oxidative damage, particularly during vulnerable growth stages. Under such conditions, approximately 1–2 % of cellular oxygen undergoes incomplete reduction, generating ROS including superoxide anions (O₂^{•−}), hydrogen peroxide (H₂O₂), hydroxyl radicals (•OH) and singlet oxygen (¹O₂). When ROS accumulation exceeds cellular detoxification capacity, widespread molecular damage ensues encompassing protein oxidation, lipid peroxidation, nucleic acid degradation, enzyme inactivation, tissue necrosis and accelerated senescence (63).

To counteract oxidative stress, plants deploy an integrated antioxidant defence network comprising enzymatic components superoxide dismutase (SOD), catalase (CAT), peroxidases (POX), ascorbate peroxidase (APX), glutathione peroxidase (GPX) and glutathione reductase (GR) alongside non-enzymatic molecules such as ascorbate and glutathione, thereby restoring carotenoids and flavonoids. Within this defence system, melatonin has emerged as a particularly potent antioxidant, operating through both direct and indirect protective mechanisms. It directly neutralises free radicals while simultaneously elevating endogenous antioxidant pools including glutathione and ascorbic acid thereby restoring cellular redox equilibrium (64). At the transcriptional level, melatonin upregulates genes encoding key antioxidant enzymes including SOD, CAT, APX and GPX under stress conditions. Previous researchers established that melatonin activates the Asada Halliwell pathway, resulting in more efficient ROS detoxification (65), while another study demonstrated that melatonin-mediated enhancement of GPX activity accelerates the removal of hydrogen peroxide and lipid peroxides during stress exposure (66).

The amphiphilic character of melatonin enables its rapid diffusion across biological membranes, allowing it to confer protection against oxidative injury across multiple cellular compartments (67). By reinforcing antioxidant enzyme activities, melatonin preserves membrane stability and maintains overall cellular integrity under adverse conditions (68). Reductions in ROS accumulation following melatonin treatment have been documented across a wide range of crop species, including rapeseed (69), wheat (70), tomato (71), cabbage (72), rice (73) and barley (74). Taken together, these findings underscore the central role of melatonin in sustaining oxidative homeostasis and enhancing plant resilience to abiotic stress.

Melatonin in secondary metabolite modulation under stress

Abiotic stresses markedly impair the synthesis and accumulation of both primary metabolites (e.g., carbohydrates, amino acids and proteins) and secondary metabolites (e.g., phenolics and flavonoids), thereby disrupting plant growth, metabolic homeostasis and adaptive capacity. Exogenous melatonin application particularly through foliar delivery has been shown to effectively counteract these deficits by stimulating metabolite accumulation and enhancing metabolic flexibility under stress conditions. Through these actions, melatonin promotes the build-up of amino acids, soluble sugars, sugar alcohols and secondary metabolites that collectively serve functions in osmotic adjustment, antioxidant defence and energy metabolism (75). At the pathway level, melatonin modulates several core metabolic routes including glycolysis, the oxidative pentose phosphate pathway and the tricarboxylic acid (TCA) cycle, thereby reinforcing carbon metabolism and energy production under adverse conditions (76). Elevated glycolytic flux under melatonin treatment generates the ATP and carbon skeletons required for downstream lipid and protein biosynthesis. In rice and tomato, melatonin-treated plants exhibited increased accumulation of amino acids, soluble sugars and polyols key intermediates supporting stress adaptation and metabolic stability (77).

Among stress-protective metabolites, proline accumulation is particularly responsive to melatonin signalling under abiotic stress. Proline contributes to osmotic adjustment, membrane stabilisation and cellular hydration during periods of stress exposure. Melatonin also drives the accumulation of soluble sugars including glucose, fructose, sucrose and trehalose which participate in osmotic regulation and energy provision under drought conditions (78). Beyond metabolite accumulation, melatonin upregulates the expression of genes governing sucrose metabolism and transport, encompassing sucrose synthase, invertase, fructokinase, phosphatase and sucrose transporter genes. In apple, melatonin-induced expression of *MdFRK2* elevated glucose, fructose and sucrose levels, thereby sustaining leaf growth and development under unfavorable conditions (79).

Melatonin further stimulates the biosynthesis of secondary metabolites and specialized antioxidant compounds. In *Carya cathayensis* Sarg. subjected to drought stress, foliar melatonin application activated metabolic pathways associated with carbon and sugar metabolism, carotenoid biosynthesis, chlorophyll turnover and phenylpropanoid production (80). Metabolomic profiling in cassava demonstrated that melatonin regulated the accumulation of over 50 distinct metabolites spanning amino acids, fatty acids, phenols, flavonoids and coumarins many of which were undetectable in salt-stressed plants that received no melatonin treatment (41). Additionally, melatonin stimulated polyamine biosynthesis including spermidine, spermine and putrescine through activation of arginine and ornithine metabolic pathways. Comparable melatonin-mediated enhancement of secondary metabolite profiles has been reported in cucumber, pigeon pea and *Dracocephalum kotschy* Boiss (81).

Field applications and practical considerations of phytomelatonin in agriculture

Phytomelatonin has emerged as a promising plant biostimulant with considerable potential for improving crop productivity and resilience under adverse environmental conditions. Numerous studies have

demonstrated that exogenous application of phytomelatonin enhances plant performance under drought, salinity, extreme temperatures, heavy metal toxicity and other abiotic stresses by improving antioxidant defence, maintaining photosynthetic efficiency and regulating stress-responsive pathways. These findings indicate that phytomelatonin could serve as an environmentally friendly approach for sustainable crop production. The effectiveness of phytomelatonin depends on several factors, including crop species, developmental stage, stress intensity and application dosage. Experimental studies have reported beneficial effects over a broad concentration range, generally between 20 and 200 μM , although the optimum concentration varies among plant species and environmental conditions (49).

Lower concentrations are often sufficient to improve seed germination and early seedling establishment, whereas relatively higher concentrations may be required to alleviate severe abiotic stress. Several methods have been employed for phytomelatonin application, including seed priming, foliar spraying, root irrigation, nutrient solution supplementation and postharvest fruit dipping (31). Among these, seed priming and foliar spraying are the most widely adopted because they are simple, economical and compatible with existing crop management practices. Seed priming enhances seed germination, seedling vigour and early stress tolerance, whereas foliar application improves photosynthetic performance, antioxidant enzyme activity and biomass accumulation under stress conditions. Despite encouraging laboratory and greenhouse studies, the commercial utilisation of phytomelatonin remains limited. Although several experimental formulations have shown promising results, only a limited number of phytomelatonin-based products are currently available for agricultural use. Further studies are needed to improve formulation stability, optimise delivery systems and evaluate long-term storage and field performance before commercialisation on a wider scale (75).

The economic feasibility of phytomelatonin application also requires further investigation. While many studies have reported improvements in plant growth, yield and stress tolerance, comprehensive cost-benefit analyses under large-scale field conditions are still lacking. Multi-location field trials are therefore necessary to evaluate the consistency, profitability and practical applicability of phytomelatonin-based crop management strategies under diverse agroecological conditions (40). Another important consideration is the regulatory framework governing phytomelatonin-based products. At present, regulations for plant biostimulants vary considerably among countries and specific guidelines for phytomelatonin formulations are still evolving. Standardised quality control, safety assessment, residue evaluation and product registration procedures will be essential to ensure the safe and effective use of phytomelatonin in agriculture.

Role of melatonin in improving crop yield and quality

Melatonin substantially improves crop growth, productivity and quality under abiotic stress by enhancing photosynthetic efficiency, antioxidant defence, assimilate translocation and hormonal equilibrium. Elevated photosynthetic pigment content and increased net photosynthetic rates under melatonin treatment drive greater photoassimilate production and more efficient source-to-sink partitioning, collectively contributing to yield improvement (82). Experimental evidence across diverse crop species consistently demonstrates melatonin's positive influence on yield-related

attributes. In banana, melatonin improved bunch architecture and fruit size characteristics. In tomato, fruit productivity and nutritional quality were enhanced through elevated accumulation of lycopene, ascorbic acid, β -carotene and essential mineral nutrients (83). Comparable benefits were recorded in cucumber under stress conditions, where melatonin treatment increased fruit number, individual fruit weight and total yield per plant (84). In pomegranate, melatonin stimulated sink activity, resulting in enlarged berry size, greater fruit weight and higher overall yield (85).

In field crops, melatonin similarly promotes grain yield and seed development. In soybean and maize, melatonin application strengthened photosynthetic performance, antioxidant enzyme activity, seed filling efficiency, seed weight and overall productivity (86). In rice, melatonin sustained productivity by delaying leaf senescence and preserving photosynthetic efficiency through modulation of ROS levels. In soybean under salinity stress, melatonin pretreatment enhanced pod formation, seed set and grain yield (87).

Beyond yield, melatonin demonstrably improves crop quality and nutritional composition. In rapeseed (*Brassica napus* L.), seed priming with melatonin improved oil quality under salinity stress by elevating unsaturated fatty acid content particularly oleic and linolenic acids while simultaneously reducing glucosinolate and saturated fatty acid levels (88). In mustard, melatonin application significantly increased seed yield, thousand-seed weight and seed oil concentration (89). Foliar melatonin treatment in *Moringa oleifera* Lam. improved amino acid profile, glutamic acid content and mineral nutrition including nitrogen, phosphorus, potassium, calcium and magnesium under drought stress (90). In flax, melatonin treatment elevated total phenolic content, soluble solids, proline and free amino acid concentrations (90). Melatonin also promotes the biosynthesis of economically valuable secondary metabolites and essential oils in medicinal plants. Under stress conditions, melatonin application increased essential oil yield in rosemary, while foliar application in lemon verbena (*Lippia citriodora* Paláu) significantly improved both overall yield and essential oil content (91).

Melatonin-mediated tolerance to abiotic stresses

Throughout their life cycle, plants are continually subjected to a range of abiotic stresses including drought, salinity, extreme temperatures, flooding and heavy metal toxicity. To persist under such adverse conditions, plants activate a repertoire of biochemical, physiological and molecular defence mechanisms. Among the diverse signalling molecules implicated in stress adaptation, melatonin has gained recognition as a pivotal regulator of plant tolerance across multiple abiotic stress scenarios. Drought and high-temperature stress impede water movement within plant tissues, disrupting transpiration, gas exchange and cellular water homeostasis (92). Under these circumstances, stomatal regulation assumes critical importance, as stomata govern both transpirational water loss and CO₂ uptake necessary for photosynthetic carbon assimilation. The ABA serves as the primary stress-responsive hormone driving stomatal closure during adverse conditions (93). While this closure curtails water loss, it simultaneously restricts CO₂ entry and diminishes overall photosynthetic efficiency, creating a physiological trade-off between water conservation and carbon gain.

Exogenous melatonin application mitigates stress-induced impairment by modulating ABA metabolism and restoring stomatal functionality. In sweet corn, melatonin treatment improved stomatal conductance and transpiration rate while reducing oxidative damage under stress conditions (94). These improvements were linked to enhanced ABA catabolism and suppression of ABA biosynthetic activity, collectively lowering endogenous ABA levels. Melatonin-treated plants additionally demonstrated improved canopy temperature regulation, attributable to enhanced transpirational cooling driven by greater stomatal conductance (95). Given that water use efficiency is intrinsically linked to stomatal conductance, transpiration rate and intercellular CO₂ assimilation (96), melatonin-mediated optimisation of these interconnected physiological processes makes a substantial contribution to plant stress tolerance under adverse environmental conditions. The regulatory influence of melatonin on plant responses across various abiotic stress conditions is illustrated in Fig. 2. Representative studies demonstrating the effects of phyto-melatonin application on different crop species, including the stress type, melatonin concentration, application method and major observed improvements, are summarised in Table 3.

Drought stress mitigation

Melatonin substantially enhances plant tolerance to drought stress through coordinated regulation of photosynthesis, stomatal behavior, antioxidant defence and water conservation mechanisms. Under water deficit conditions, melatonin shields the photosynthetic apparatus by reducing chlorophyll degradation and sustaining photosynthetic efficiency, transpiration and stomatal conductance. Melatonin treatment elevates the photochemical efficiency (Fv/Fm) of photosystem II (PSII) and the electron transport rate (ETR), thereby preserving photosynthetic activity throughout the period of drought exposure (97). In maize, melatonin application maintained higher relative water content and protected chloroplast structural integrity under water deficit conditions. The enhancement of stomatal conductance induced by melatonin facilitates improved movement of both water vapor and CO₂, collectively supporting continued photosynthesis and plant growth under stress (98).

Melatonin further modulates ABA metabolism under drought conditions by upregulating ABA catabolic genes such as *MdCYP707A1* while simultaneously suppressing the ABA biosynthetic gene *MdNCED3*, resulting in reduced endogenous ABA accumulation and improved stomatal regulation. In parallel, melatonin reinforces antioxidant defence capacity by promoting the scavenging of ROS including superoxide anions, hydrogen peroxide and hydroxyl radicals generated in excess during drought stress. It activates key antioxidant enzymes including catalase (CAT), ascorbate peroxidase (APX) and peroxidase (POD) and further regulates the ascorbate glutathione cycle, collectively reducing membrane damage, malondialdehyde (MDA) accumulation and electrolyte leakage (99). Additionally, melatonin limits non-stomatal water loss by promoting cuticular wax deposition through enhanced expression of wax biosynthesis genes *KCS1* and *LTP1*, thereby providing an additional layer of water conservation under drought conditions (100).

Salinity stress tolerance

Salt stress triggers excessive accumulation of ROS within plant cells, inflicting oxidative damage on membrane lipids, proteins and cellular structures, which ultimately restricts plant growth and development. Beyond oxidative injury, high salinity imposes

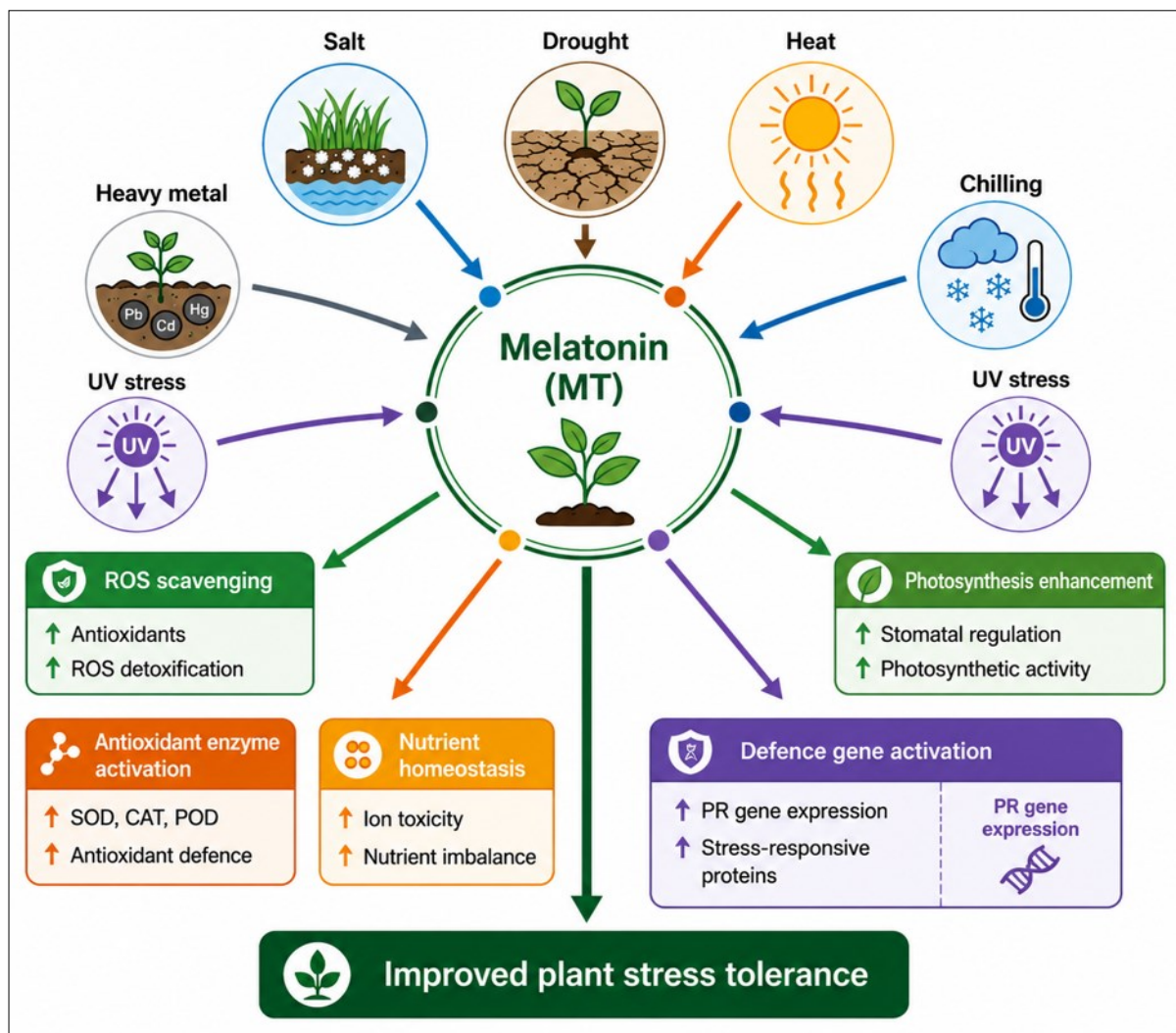


Fig. 2. Schematic representation of melatonin-mediated regulation of plant responses under various abiotic stress conditions.

osmotic stress by lowering water potential and hampering the uptake of both water and essential mineral nutrients. Under these conditions, plants initiate stomatal closure as a mechanism to minimize water loss, which in turn reduces stomatal conductance and suppresses photosynthetic activity (101). Melatonin plays a central role in enhancing salinity tolerance through integrated regulation of photosynthesis, ion homeostasis, antioxidant defence and osmotic adjustment. In grapevine seedlings, endogenous melatonin concentrations were found to increase in both leaf and root tissues in response to salinity stress (102), suggesting an active role in the plant's adaptive response. With respect to ionic balance, melatonin contributes to Na^+ and K^+ homeostasis by activating transporter genes including *NHX1* and *AKT1*, which function to sustain cytoplasmic ion equilibrium under saline conditions. In rice, melatonin reinforced salinity tolerance through NADPH oxidase-mediated regulation of potassium transporters. Combined seed priming and foliar application of melatonin in cassava improved photosynthetic rate, transpiration efficiency, osmotic adjustment, proline accumulation and soluble protein content under salt stress (103). Melatonin also promotes seed germination and broader crop performance under salinity stress. Seed priming with melatonin improved germination in melon (104) and enhanced osmotic regulation in cotton grown under saline conditions. Furthermore, beneficial effects of melatonin on stomatal conductance and transpiration mediated through ABA-dependent regulatory pathways have been documented in tomato, rice and pepper (62, 105, 106).

Temperature stress (Heat and chilling)

Both high and low temperature extremes severely impair plant growth, photosynthesis, membrane stability and overall crop productivity. Melatonin functions as an effective plant growth regulator that confers tolerance to temperature stress through coordinated regulation of antioxidant defence, photosynthetic activity, osmotic balance and stress-responsive gene expression (41). Under heat stress conditions, melatonin improves CO_2 assimilation, stimulates photosynthetic pigment synthesis and shields photosystem I and II from photoinhibitory damage in tomato (107). It further strengthens antioxidant defence including the ascorbate glutathione cycle while modulating nitric oxide and polyamine metabolism to limit oxidative injury. In wheat, melatonin elevated the expression of stress-responsive transcription factors including TaMYB80, TaWRKY26 and TaWRKY39, alongside antioxidant enzyme genes *TaCAT*, *TaPOD* and *TaSOD*. Comparable enhancements in growth, biomass accumulation, soluble sugar and protein content and antioxidant enzyme activities were recorded in maize and mung bean under heat stress (59). In rice subjected to elevated temperatures, melatonin additionally improved photosynthetic efficiency, stabilised starch biosynthesis and reduced grain chalkiness, highlighting its relevance to grain quality under thermal stress.

Under chilling stress, melatonin similarly demonstrates broad protective capacity across diverse species. In maize, melatonin enhanced cold tolerance by remodeling embryo proteome composition under low temperature conditions (108). In rice and cucumber, melatonin improved seed germination and

photosynthetic performance through modulation of ABA signalling and attenuation of membrane damage during chilling exposure. In melon and peach, melatonin reduced ROS accumulation and elevated proline, soluble protein and ascorbic acid levels, thereby alleviating chilling-induced injury (109). In tea plants and rapeseed, melatonin preserved photosynthetic pigment integrity, enhanced antioxidant capacity, regulated stress-responsive gene expression and minimised oxidative and membrane damage under low temperature conditions. Collectively, melatonin improves plant tolerance to temperature extremes by preserving membrane integrity, reinforcing antioxidant defence systems, regulating osmolyte accumulation and protecting the photosynthetic apparatus under both heat and chilling stress conditions (110).

Flooding stress tolerance

Melatonin has been established as an effective phytohormone capable of strengthening plant resilience to waterlogging stress. In apple seedlings, melatonin application enhanced waterlogging tolerance by curtailing excessive ROS accumulation, preventing mitochondrial dysfunction and sustaining both aerobic respiration and photosynthetic activity under flooded conditions (13). Comparable protective responses were observed in lucerne, where melatonin pretreatment mitigated waterlogging-induced injury through improvements in chlorophyll content, overall plant growth and PSII photochemical efficiency. Melatonin-conferred stress tolerance under flooding conditions is further linked to its regulatory influence over ethylene and polyamine metabolism. In lucerne, melatonin suppressed ethylene biosynthesis while simultaneously promoting polyamine accumulation, a combination that contributed to improved membrane stability, enhanced photosynthetic performance and reduced ethylene-driven senescence during waterlogging stress (111).

Heavy metal tolerance

Heavy metal and metalloid toxicity represents one of the most damaging abiotic stresses constraining plant growth and productivity. Toxic elements such as lead (Pb), cadmium (Cd), mercury (Hg) and the metalloid arsenic (As) disrupt normal plant metabolic processes even at relatively low concentrations (112). Exposure to these metals triggers excessive ROS generation,

culminating in oxidative stress, lipid peroxidation, membrane deterioration and broad disruption of cellular functions (75). Accumulating evidence indicates that heavy metal stress actively stimulates endogenous melatonin biosynthesis across a range of plant species, including barley, tomato, lupin, tobacco, *A. thaliana* and rice (113). Under cadmium stress specifically, severe injury to chloroplasts, mitochondria and the endoplasmic reticulum promotes the release of serotonin N-acetyltransferase (SNAT) into the cytosol, where it drives enhanced melatonin biosynthesis through increased N-acetylserotonin production (114). This stress-induced upregulation of endogenous melatonin suggests an intrinsic protective role of the molecule in plant heavy metal responses. Melatonin confers protection against heavy metal toxicity through several complementary mechanisms. It directly neutralises ROS, thereby mitigating metal-induced oxidative damage. Additionally, melatonin possesses metal chelating capacity and its amphiphilic nature enables rapid traversal of cellular membranes and accumulation across multiple subcellular compartments, substantially broadening its protective reach (115). At the whole-plant level, exogenous melatonin application has been shown to alleviate cadmium and zinc toxicity in lemon balm by reinforcing antioxidant defence systems and improving overall stress tolerance (116).

Conclusion

Phytomelatonin plays an important role in improving plant growth and enhancing tolerance to a wide range of abiotic stresses through the regulation of antioxidant defence, redox homeostasis and interactions with multiple phytohormones. These findings suggest that phytomelatonin has considerable potential for improving crop performance and supporting sustainable agricultural production under changing environmental conditions. Despite these promising developments, several challenges remain before phytomelatonin can be widely adopted in agricultural practice. Most published studies have been carried out under laboratory or greenhouse conditions, while relatively few have evaluated its effectiveness under field environments. In addition, differences in melatonin concentration, application method, treatment stage and crop

Table 3. Representative studies demonstrating the effects of phytomelatonin on crop performance under abiotic stress

Crop species	Stress type	Melatonin concentration	Application method	Key findings	References
<i>Oryza sativa</i> L. (Rice)	Salinity	20 µM	Seed priming	Improved root and shoot growth, dry weight and K ⁺ accumulation	(117)
<i>Triticum aestivum</i> L. (Wheat)	Salinity	200 µM	Seed priming	Enhanced seed germination and seedling growth	(57)
<i>Zea mays</i> L. (Maize)	Drought	100 µM	Foliar spray	Increased antioxidant enzyme activities, enhanced photosystem activity, reduced H ₂ O ₂ , superoxide and MDA	(118)
<i>Glycine max</i> (L.) Merr. (Soybean)	Nitrogen deficiency	100 µM	Foliar spray	Improved nitrogen fixation and expression of nitrogen metabolism genes	(119)
<i>Solanum lycopersicum</i> L. (Tomato)	Heavy metal (Cadmium)	100 µM	Foliar spray	Reduced Cd accumulation and enhanced antioxidant enzyme activity	(75)
<i>Malus domestica</i> (Suckow) Borkh. (Apple)	Drought	100 µM	Foliar spray	Improved nitrogen assimilation and endogenous melatonin content	(97)
<i>Camellia sinensis</i> (L.) Kuntze (Tea)	Chilling stress	100 µM	Foliar spray	Prevented oxidative damage and improved photosynthetic pigments	(110)
<i>Cucumis sativus</i> L. (Cucumber)	Chilling stress	200 µM	Foliar spray	Reduced electrolyte leakage and improved photosynthesis	(120)

species have resulted in inconsistent application protocols, making it difficult to establish standardised recommendations. Although recent studies have considerably advanced our understanding of melatonin biosynthesis and its physiological functions, the molecular mechanisms underlying melatonin perception, receptor-mediated responses and downstream signalling pathways remain incompletely understood. Future research should therefore focus on elucidating these mechanisms, including the identification and functional characterisation of additional melatonin receptors, their interacting signalling components and the transcriptional networks regulating stress-responsive genes. Furthermore, large-scale and long-term field trials across diverse agroecological conditions are needed to validate the efficacy of melatonin under realistic agricultural environments and to establish optimal crop-specific application methods, doses and timing. Further efforts to develop stable commercial formulations and appropriate regulatory guidelines will also support the practical use of phytomelatonin for improving crop productivity, abiotic stress tolerance and resilience under changing climatic conditions.

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Authors' contributions

VM collected the literature and drafted the manuscript, while GA provided overall guidance and revised the manuscript. SE, AP and SKG assisted with literature collection and formatting. All authors have read and approved the final manuscript.

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