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REVIEW

Melatonin-Mediated Coordination of ROS Signaling, Physiological, and Hormonal Networks under Drought Stress

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ABSTRACT: Drought stress stands out as a main abiotic factor that adversely influences the development, yield, and quality of plants. With the increasing prevalence of water scarcity driven by climate change, urban expansion, and industrial activities, understanding plant responses to limited water availability has become critically important. Among stress-related molecules, melatonin has gained recognition as a multipurpose regulator with a central role in strengthening plant tolerance to drought. The synthesis and accumulation of melatonin are influenced by environmental stressors and vary across plant species and tissue types. Whether synthesized internally or applied externally, melatonin contributes to drought mitigation by neutralizing reactive oxygen species (ROS), boosting the activity of enzymatic antioxidants, and modulating levels of non-enzymatic defense compounds. Additionally, it regulates stress-responsive genes and activates defense pathways intermediated by key phytohormones such as abscisic acid (ABA), salicylic, and gibberellins. Melatonin's interaction with other hormonal signals including auxins, cytokinins, jasmonates, and ethylene creates a dynamic network of hormonal crosstalk that further strengthens plant tolerance mechanisms. Its beneficial effects are evident in improved photosynthetic efficiency, optimized stomatal behavior, enhanced seed germination, and stimulated root development. This review focus on the effects of melatonin in plants under drought conditions, highlighting its interplay with other signaling molecules and hormonal pathways. It further highlights recent progress and strategic approaches for utilizing melatonin in developing drought-resilient cultivars and enhancing agricultural sustainability.

KEYWORDS: Bio-stimulants; hormonal crosstalk; photosynthesis; growth regulators; plant resilience; water scarcity

1 Introduction

Global agricultural systems are increasingly challenged by the need to meet rising food demands under intensifying environmental constraints. Among the major abiotic stressors, drought represents a predominant limitation that severely disrupts plant growth, productivity, and crop quality [1]. Water deficit induces complex physiological and metabolic disturbances, including impaired photosynthetic efficiency, disruption of osmotic regulation, altered nutrient balance, and excessive accumulation of reactive oxygen species (ROS), ultimately leading to growth inhibition and yield reduction [1–3].

To cope with these environmental constraints, plants have evolved sophisticated adaptive mechanisms operating at morphological, physiological, and molecular levels. These include modulation of root architecture to enhance water uptake, regulation of stomatal conductance to optimize water use efficiency [4–6], and

activation of osmotic adjustment processes to maintain cellular turgor under water-limited conditions [7,8]. At the molecular level, drought responses are tightly regulated by highly coordinated phytohormonal networks that integrate growth and stress signaling pathways. Key regulatory hormones involved in these processes include abscisic acid (ABA), auxins, cytokinins, gibberellins, ethylene, jasmonates, salicylic acid, and strigolactones, which collectively orchestrate plant adaptive responses to environmental stress [9,10]. The dynamic crosstalk among these signaling pathways enables plants to fine-tune the balance between growth maintenance and stress acclimation under drought conditions.

In this regulatory framework, melatonin, an indole-derived molecule synthesized from serotonin (5-hydroxytryptamine), was first identified in the bovine pineal gland [11]. In plants, melatonin has emerged as a multifunctional regulator that interacts extensively with major phytohormones, including IAA, GA, ABA, brassinosteroids, strigolactones, and polyamines, particularly under drought stress conditions [12,13]. Melatonin also modulates the activity of key enzymes, receptors, and transcription factors involved in hormone biosynthesis and signal transduction pathways. Mechanistically, melatonin enhances drought tolerance through the maintenance of cellular redox homeostasis by directly scavenging reactive oxygen species and by stimulating the antioxidant defense system, including both enzymatic and non-enzymatic components [14,15]. In addition, it regulates osmotic adjustment, stabilizes cellular structures, and preserves membrane integrity under water deficit conditions. Its auxin-like activity further contributes to growth regulation, as demonstrated in adventitious rooting of *Prunus cerasus* shoot tip explants and root proliferation in *Brassica juncea* [16]. Through its integration into phytohormonal crosstalk networks, melatonin coordinates signaling pathways, gene expression, and post-transcriptional regulation, thereby enhancing plant adaptation to drought stress. These processes involve regulation of melatonin biosynthesis, degradation, transport, receptor interactions, and downstream signal transduction pathways [17].

Acting as a versatile regulatory molecule, melatonin influences both plant growth and developmental processes. Recent studies highlight its role in mitigating multiple environmental stresses, including salinity [18], chilling [19], and drought [20], while also regulating key developmental processes such as flowering, senescence, and overall growth progression [21]. Moreover, melatonin enhances both the activity and transcriptional regulation of antioxidant systems, thereby strengthening plant resilience against abiotic and biotic stresses. As a naturally occurring and non-toxic compound, melatonin has gained increasing attention as a sustainable biostimulant in agriculture. Its ability to enhance crop productivity and quality with minimal environmental impact makes melatonin a promising alternative to synthetic agrochemicals. Growing interest in sustainable agriculture has accelerated research on melatonin biosynthesis, distribution, and signaling pathways, highlighting its multifaceted role in plant stress adaptation. This review summarizes the biosynthesis and distribution of melatonin and its regulatory role in drought stress tolerance, while also discussing future prospects for its application in sustainable agriculture.

2 Drought Effects on Plants

Plant growth, productivity and quality are significantly hindered by various biotic and abiotic stressors [22–24]. Drought stress represents one of the most severe abiotic constraints limiting global agricultural sustainability, particularly in horticultural production systems, where yield and quality traits are highly sensitive to water availability [25,26]. Water deficit induces a cascade of interlinked physiological, biochemical, and molecular disturbances that collectively impair plant growth and productivity across developmental stages [27]. At the physiological level, drought restricts photosynthetic carbon assimilation primarily through stomatal closure, reduced CO_2 diffusion, and subsequent suppression of Calvin cycle activity, leading to decreased carbon fixation efficiency and enhanced photorespiration (Fig. 1). These limitations

are further exacerbated by degradation of photosynthetic pigments and disruption of electron transport processes, ultimately resulting in over-reduction of the photosynthetic apparatus and excessive generation of ROS in chloroplasts and mitochondria. Elevated ROS levels, including hydrogen peroxide, promote lipid peroxidation, protein oxidation, and membrane destabilization, thereby accelerating cellular dysfunction and senescence processes [28].

Concomitantly, drought stress disrupts plant water relations by reducing relative water content, impairing osmotic adjustment, and altering nutrient acquisition and transport [29]. These physiological constraints manifest at the whole-plant level as reduced biomass accumulation, inhibited vegetative growth, delayed flowering, and decreased fruit set. In horticultural crops, such impairments translate into smaller fruit size, reduced flavor quality, shortened shelf life, and increased susceptibility to postharvest decay [30,31]. Hormonal imbalance particularly involving ABA-mediated stress signaling and premature senescence further aggravate yield losses, while also increasing production costs and reducing marketable yield, thereby posing significant economic and environmental challenges [32].

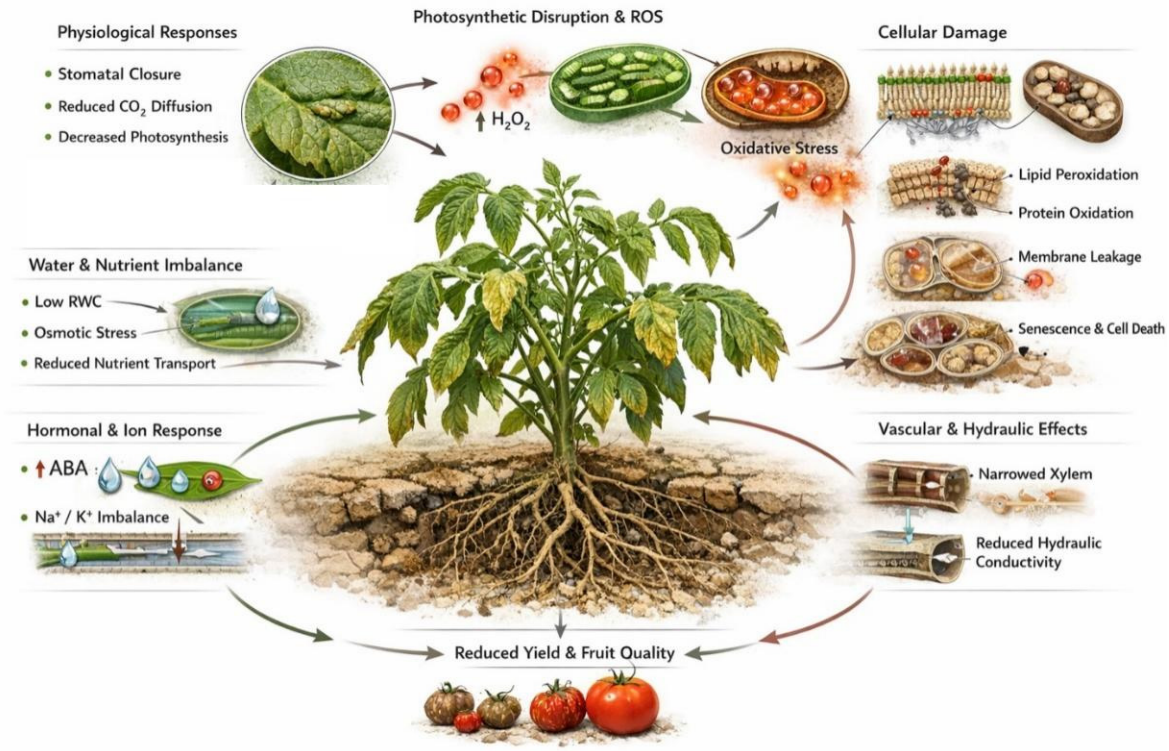

Figure 1: Integrated Physiological, Biochemical, and Structural Impacts of Drought Stress on plants.

At the morphological level, drought induces adaptive and stress-associated modifications, including reduced leaf expansion, leaf rolling, senescence, and abscission, followed by a progressive decline in biomass accumulation. These adjustments may also represent an energy-saving strategy, enabling plants to reduce transpiration demand and conserve internal resources under water-limited conditions [33]. Root system remodeling, including enhanced root-to-shoot ratio, is a key adaptive trait that improves water foraging capacity under soil moisture deficit [34]. From a structural and cellular perspective, drought stress induces progressive tissue-level damage, including leaf tip burn, chlorosis, necrosis, bronzing, twig dieback, and eventual tissue collapse [35]. At the vascular level, water deficit alters xylem hydraulics by reducing vessel

diameter and hydraulic conductivity, thereby increasing resistance to water transport and limiting nutrient movement within the plant system.

In parallel, drought stress disrupts ionic homeostasis, particularly affecting Na^+ and K^+ balance due to altered membrane transport and reduced selectivity in ion uptake systems [36]. Maintenance of ion equilibrium is critical for enzymatic activity, osmotic stability, and cellular function under stress conditions. High-affinity potassium transporters and specialized membrane proteins play essential roles in regulating ion fluxes and maintaining Na^+/K^+ homeostasis, thereby supporting plant survival and productivity under stress conditions [37]. Comparative studies further indicate that drought tolerance varies significantly among plant functional groups, with halophytes generally exhibiting enhanced resilience due to specialized root architecture, improved stomatal regulation, and greater metabolic plasticity. Although primarily adapted to salinity, halophytes often display cross-tolerance to drought stress, suggesting shared adaptive mechanisms between abiotic stress responses [38]. Drought stress imposes multi-level constraints on horticultural crop performance by integrating physiological limitations, oxidative damage, hydraulic failure, and ionic imbalance, ultimately leading to substantial reductions in yield and quality. Understanding these interconnected mechanisms is essential for developing strategies aimed at improving crop resilience under water-limited environments. Experimental studies clearly demonstrate that declining soil moisture directly impairs plant water relations [39]. In grapevine, drought conditions significantly reduced leaf water content, hydraulic conductivity, and turgor maintenance, leading to visible leaf wilting and reduced growth [40]. Recent experimental evidence confirms that plant responses are strongly dependent on quantitative reductions in soil moisture, which induce progressive physiological disruptions rather than binary stress responses [39].

Experimental studies in different crops clearly demonstrate that declining soil moisture directly impairs plant water relations. In grapevine, drought conditions significantly reduced leaf water content, hydraulic conductivity, and turgor maintenance, leading to visible leaf wilting and reduced growth. Importantly, grafted grapevines maintained higher water status under drought, indicating that root-mediated hydraulic regulation is a key tolerance mechanism [40]. Similarly, in tomato, controlled deficit irrigation treatments revealed that reductions in soil moisture availability directly limit water uptake and fruit development, particularly under severe drought ($\leq$12.5% soil water content), where cellular dehydration constrains fruit expansion. These findings reinforce that hydraulic failure is one of the earliest and most critical constraints under drought in fleshy horticultural crops [39].

Drought-induced stomatal closure is consistently observed across different crops. In grapevine, water deficit triggered rapid stomatal closure, leading to reduced photosynthetic capacity and chlorophyll content, which ultimately constrained biomass accumulation [40]. In greenhouse tomato systems, deficit irrigation significantly decreased photosynthesis and fruit yield, confirming the tight coupling between stomatal regulation and carbon assimilation under water limitation [41]. However, under mild drought (50% irrigation), tomato plants were able to maintain or even improve water-use efficiency (WUE) without major yield penalties, indicating an adaptive stomatal optimization strategy [42]. Recent experimental work in tomato demonstrated that drought stress induces a strong shift in redox metabolism. Under moderate water deficit, antioxidant activity (e.g., phenolics, TEAC, DPPH) increased, suggesting an adaptive ROS-scavenging response. However, under severe drought, oxidative imbalance was associated with declines in carotenoids (lycopene, β-carotene) and disruption of cellular homeostasis [39]. In grapevine, drought similarly reduced chlorophyll content and enhanced oxidative stress markers, confirming that ROS overproduction is a conserved response across fruit crops. These oxidative processes are directly linked to quality deterioration, including pigment loss and impaired nutritional value in fruits and vegetables [40].

3 Melatonin Biosynthesis and Signaling

Melatonin biosynthesis in plants is a highly regulated process influenced by both environmental cues and developmental signals. Light represents a major regulator of melatonin production, with its synthesis being differentially induced across various plant organs in response to environmental stimuli [43]. Developmental stages, including fruit development [44] and leaf growth [45], also significantly modulate melatonin accumulation. In addition, abiotic stress conditions such as drought, low temperature [46], and heat [43] strongly stimulate melatonin biosynthesis, highlighting its role as a stress-responsive signaling molecule. At the biochemical level, melatonin biosynthesis originates from tryptophan and proceeds through a series of well-defined enzymatic steps. The primary pathway begins with the decarboxylation of tryptophan into tryptamine, catalyzed by tryptophan decarboxylase (TDC). Tryptamine is subsequently hydroxylated by tryptamine 5-hydroxylase (T5H) to form serotonin (5-hydroxytryptamine), which serves as a central intermediate in the pathway. Alternatively, tryptophan may first undergo hydroxylation to 5-hydroxytryptophan, followed by decarboxylation via aromatic-L-amino-acid decarboxylase or TDC, ultimately converging at serotonin formation (Fig. 2). Following serotonin synthesis, serotonin N-acetyltransferase (SNAT) catalyzes its conversion into N-acetylserotonin, which is subsequently methylated by N-acetylserotonin methyltransferase (ASMT) or hydroxyindole-O-methyltransferase (HIOMT) to yield melatonin. An alternative route involves methylation of serotonin to 5-methoxytryptamine by HIOMT, followed by acetylation via SNAT to form melatonin [47]. In contrast, a less common pathway involving direct acetylation of tryptamine produces N-acetyltryptamine; however, this route is limited because T5H cannot convert N-acetyltryptamine into N-acetylserotonin [14]. Additionally, a reverse reaction has been proposed in which N-acetylserotonin is deacetylated to regenerate serotonin, suggesting dynamic regulation of intermediate pools within the pathway [48]. Notably, melatonin shares a common precursor (tryptophan) with indole-3-acetic acid (IAA), linking its biosynthesis to auxin metabolism. While melatonin synthesis proceeds via tryptamine formation, IAA biosynthesis involves conversion to indole-3-acetaldehyde, indicating metabolic competition and coordination between these pathways. This shared origin underpins functional interactions between melatonin and auxin in regulating plant growth and stress responses [46].

Subcellular compartmentalization further adds complexity to melatonin biosynthesis. Although chloroplasts are considered the primary sites of melatonin production, its synthesis also occurs in mitochondria, cytosol, and nucleus, suggesting a multi-organelle regulatory system that enables rapid and localized responses to environmental changes [49]. At the genetic level, key biosynthetic genes such as *TDC*, *T5H*, *SNAT*, and *ASMT* have been identified in several plant species, including mulberry, where MnTDC, MnT5H2, MnSNAT5, and MnASMT12 are implicated in melatonin production [50]. Environmental signals including light, temperature, drought, and salinity modulate the expression and activity of these enzymes; however, the precise regulatory mechanisms controlling this modulation remain incompletely understood [51]. Beyond its biosynthesis, melatonin functions as a signaling molecule through interactions with specific receptor-like systems. Evidence suggests that melatonin perception involves G protein-coupled receptor-like proteins and calmodulin-associated signaling components, which initiate downstream signaling cascades regulating gene expression and stress responses [37,52].

In addition, melatonin has been reported to interact with the auxin receptor TIR1, thereby modulating auxin signaling pathways and influencing plant growth and development [37]. Functionally, melatonin integrates into multiple physiological and molecular processes that enhance plant performance under both normal and stress conditions. It modulates fruit ripening, improves crop quality, and enhances resistance to stress [53]. Melatonin delays senescence and maintains chloroplast integrity, as demonstrated in broccoli, where it inhibits chlorophyll degradation and prolongs storage quality [54]. At the molecular

level, melatonin regulates stress-responsive gene expression by upregulating genes encoding antioxidant enzymes and molecular chaperones, thereby enhancing cellular protection mechanisms. In crops such as tomato, melatonin increases the activity of antioxidant enzymes including superoxide dismutase (SOD) and peroxidase (POD), mitigating oxidative damage induced by drought, heat, and cold stress [55]. Similarly, melatonin improves photosynthetic efficiency and reduces oxidative stress through transcriptional activation of antioxidant-related genes [56,57].

Furthermore, melatonin modulates the expression of key photosynthesis-related genes [58], including *RCA*, *SBPase*, *rbcL*, *psaA*, *psaB*, and *psbB*, thereby sustaining photosynthetic capacity under stress conditions [59]. This transcriptional regulation supports efficient energy metabolism, enhances ROS detoxification, and promotes synthesis of protective proteins such as molecular chaperones. In addition, melatonin engages in complex hormonal crosstalk, particularly with ABA-dependent signaling pathways [60], contributing to coordinated stress responses and improved plant resilience.

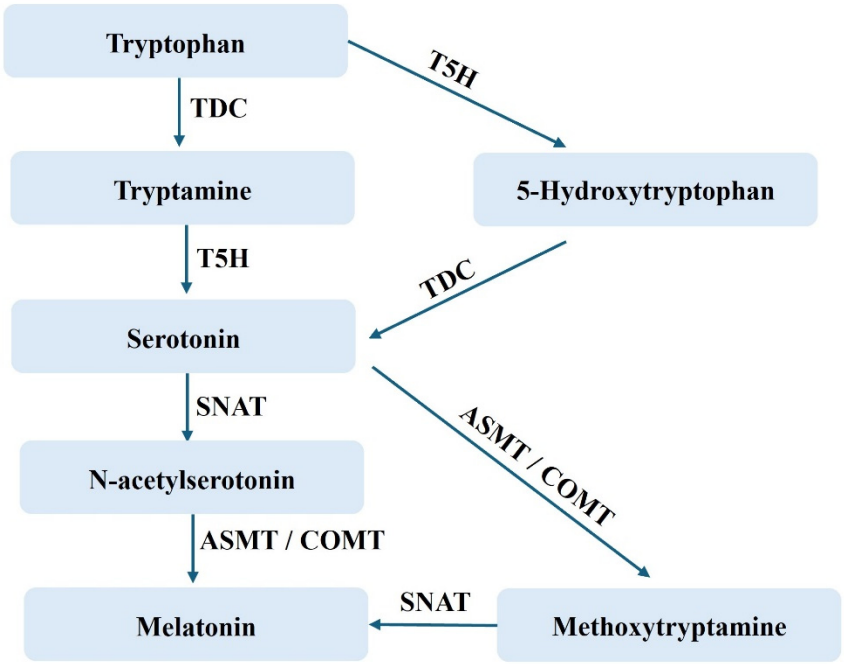

Figure 2: The biosynthetic pathways of phytomelatonin. The diagram illustrates the metabolic flexibility of melatonin synthesis in plants, starting from the precursor tryptophan. The process involves several enzymatic routes, including the classical conversion via tryptamine and an alternative route through 5-Hydroxytryptophan. Both pathways converge at Serotonin, which is then converted into melatonin through two distinct branches, the standard acetylation-first route involving N-acetylserotonin, and a stress-responsive methylation-first route via Methoxytryptamine. These pathways are mediated by key enzymes including TDC (tryptophan decarboxylase), T5H (tryptophan 5-hydroxylase), SNAT (serotonin N-acetyltransferase), and ASMT/COMT (N-acetylserotonin O-methyltransferase/caffeic acid O-methyltransferase).

4 Physiological and Molecular Mechanisms of Melatonin

Extensive research has established melatonin as a central regulator of plant adaptive responses to drought stress, functioning through highly integrated signaling networks that coordinate redox homeostasis, hormonal crosstalk, and transcriptional reprogramming. A key milestone in elucidating melatonin signaling was the identification of the phytomelatonin receptor AtPMTR1 in *Arabidopsis thaliana*, which exhibits struc-

tural similarity to G protein-coupled receptors and interacts with the G protein α subunit (GPA1), thereby linking melatonin perception to core stress signaling pathways [61]. Activation of PMTR1 triggers downstream signaling cascades involving NADPH oxidase-dependent ROS generation and mitogen-activated protein kinase (MAPK) pathways, which collectively regulate stomatal movement and stress-responsive gene expression [23,61].

Recent studies further indicate that melatonin-mediated ROS production functions as a controlled signaling event rather than merely oxidative damage, acting as a secondary messenger to activate MAPK cascades and Ca^{2+} signaling pathways, thereby fine-tuning stomatal closure and enhancing drought-induced stomatal immunity [62,63]. Through these mechanisms, melatonin optimizes gas exchange while minimizing transpirational water loss under water-deficit conditions. At the molecular level, melatonin activates MAPK signaling modules (e.g., MPK3/MPK6), leading to phosphorylation of transcription factors that regulate genes involved in root development, osmotic adjustment, and stress tolerance [2,6,61]. This transcriptional reprogramming is further supported by epigenetic and post-transcriptional regulation, including modulation of microRNAs and chromatin remodeling factors, which enhance plant adaptability under prolonged drought stress [20].

Melatonin also integrates into lipid-derived signaling pathways, acting upstream of phospholipid metabolism. It stimulates phospholipase D (PLD)-mediated hydrolysis of phosphatidylcholine, generating phosphatidic acid (PA), a central lipid signaling molecule that interacts with protein phosphatase 2A, NADPH oxidases, and nitric oxide signaling pathways [64]. PA has also been shown to regulate membrane trafficking and vesicle dynamics under stress conditions, thereby contributing to cellular homeostasis [65]. In parallel, melatonin enhances phospholipase C (PLC) activity, leading to the hydrolysis of phosphatidylinositol 4,5-bisphosphate and the production of inositol trisphosphate (IP_3), which triggers intracellular Ca^{2+} release. Elevated cytosolic Ca^{2+} activates calmodulin and calcium-dependent protein kinases (CDPKs), amplifying downstream stress signaling and coordinating adaptive responses such as root growth and stomatal regulation [64].

These signaling pathways converge to regulate plant morphology, particularly root system architecture. Melatonin has been shown to promote lateral and adventitious root formation in species such as cucumber [66], thereby enhancing soil water exploration and improving water-use efficiency under drought stress [67]. Recent findings suggest that this effect is mediated through crosstalk with auxin transporters (PIN proteins) and modulation of auxin gradients, further highlighting the integrative role of melatonin in growth regulation.

A central component of melatonin-mediated drought tolerance is the regulation of cellular redox homeostasis. Melatonin enhances antioxidant defense systems through MAPK-dependent transcriptional activation of genes encoding key antioxidant enzymes, resulting in increased activities of SOD, CAT, POD, and APX, along with elevated levels of non-enzymatic antioxidants such as ascorbic acid and glutathione. Importantly, melatonin also regulates the ascorbate–glutathione cycle and maintains NADPH availability, thereby sustaining redox buffering capacity under stress conditions [68]. This coordinated antioxidant network effectively reduces ROS, nitric oxide (NO), and hydrogen peroxide (H_2O_2) accumulation, limiting oxidative damage and preserving cellular integrity [69,70].

Melatonin plays a pivotal role in plant drought adaptation through the regulation of ion homeostasis, membrane transport systems, and ROS-mediated signaling pathways. Under drought stress, melatonin modulates the activity of several ion channels and transporters involved in stomatal regulation and cellular osmotic adjustment, including Ca^{2+}, K^+, Cl^-, and H^+-ATPase transport systems [71]. These regulatory actions contribute to the maintenance of guard cell turgor, optimization of stomatal aperture, and improve-

ment of water-use efficiency under limited water availability [42]. Emerging evidence also indicates that melatonin influences vacuolar ion sequestration and membrane stability, thereby supporting intracellular osmotic balance and cellular hydration during dehydration stress.

A critical component of melatonin-mediated signaling involves the modulation of NADPH oxidase (respiratory burst oxidase homologs; RBOHs), which function as major sources of stress-induced ROS production. By fine-tuning ROS generation, melatonin acts upstream of ROS-sensitive ion channels and transporters that participate in calcium signaling, stomatal movement, and stress-responsive signal transduction [72]. This controlled ROS signaling network enables plants to maintain redox homeostasis while simultaneously activating adaptive physiological responses. Furthermore, the interaction between melatonin, ROS signaling, and ion transport systems establishes an integrated regulatory framework that enhances drought tolerance through coordinated control of stomatal dynamics, osmotic adjustment, and cellular protection mechanisms. Beyond antioxidant regulation, emerging evidence highlights the role of melatonin in mitochondrial and chloroplast protection, where it stabilizes electron transport chains, reduces electron leakage, and prevents excessive ROS generation at the source [73]. Additionally, melatonin influences energy metabolism by maintaining ATP production and regulating carbon partitioning under drought stress, thereby sustaining metabolic activity and growth. Melatonin-mediated signaling integrates receptor activation, ROS and MAPK cascades, lipid and calcium signaling, transcriptional and epigenetic regulation, and antioxidant defense systems into a unified network. This multi-layered regulatory framework enables plants to dynamically respond to drought stress, optimizing growth, maintaining cellular homeostasis, and enhancing overall stress resilience [73]. The effectiveness of melatonin-mediated drought tolerance may vary depending on stress severity [74]. Under mild water deficit, melatonin primarily supports stomatal regulation, photosynthetic maintenance, and antioxidant activation to preserve normal metabolic activity. In contrast, under severe drought stress, melatonin promotes stronger osmotic adjustment, enhanced ROS detoxification, membrane stabilization, and stress-responsive gene activation to minimize cellular damage and maintain survival [75]. These findings suggest that melatonin-mediated responses are highly dynamic and dependent on drought intensity and duration.

5 Modulatory Role of Melatonin in Stress-Responsive Gene Networks

Melatonin plays a pivotal role in modulating stress-responsive gene networks that underpin plant adaptation to drought stress. It regulates a broad spectrum of genes associated with metabolic homeostasis, redox balance, osmotic adjustment, and hormonal signaling, thereby enhancing the plant's capacity to withstand water deficit conditions (Table 1). Exogenous melatonin application has been shown to significantly reprogram transcriptomic profiles under drought stress, leading to coordinated activation of drought-associated genes and stabilization of cellular metabolism [76,77].

At the metabolic level, melatonin induces the expression of genes involved in nitrogen assimilation, including glutamine synthetase, thereby enhancing nitrogen use efficiency and sustaining amino acid biosynthesis under water-limited conditions. This transcriptional regulation supports enzymatic activity and contributes to maintaining biomass accumulation despite reduced water availability [77]. In addition, genotype-specific responses have been observed, as demonstrated in fenugreek, where melatonin-induced upregulation of the CAS gene in the Shushtar landrace was associated with increased accumulation of steroidal saponins and improved drought tolerance, while minimizing biomass loss [78]. Beyond nitrogen metabolism, melatonin orchestrates the expression of genes involved in carbon metabolism and photosynthetic maintenance, ensuring continued energy production under stress conditions [79]. It also enhances the

transcription of genes encoding antioxidant enzymes and osmoprotectant biosynthesis pathways, thereby reinforcing cellular defense systems against oxidative and osmotic stress [12].

Recent transcriptomic and functional genomics studies further reveal that melatonin regulates key stress-responsive transcription factors, including members of the WRKY, NAC, MYB, and DREB families, which act as central nodes in drought signaling networks [80,81]. Through these transcription factors, melatonin integrates upstream signaling events such as ROS, Ca^{2+}, and MAPK cascades into downstream gene expression programs that control stress adaptation.

In addition to transcriptional regulation, emerging evidence highlights the role of melatonin in post-transcriptional and epigenetic control mechanisms. Melatonin has been shown to modulate microRNA expression profiles, thereby influencing mRNA stability and translation efficiency of stress-responsive genes. Furthermore, it may contribute to chromatin remodeling and histone modifications, facilitating rapid and reversible gene expression changes under fluctuating environmental conditions. Importantly, melatonin-mediated gene regulation is closely linked with hormonal signaling pathways. It modulates ABA-responsive genes involved in stomatal regulation and drought perception, while also interacting with auxin- and cytokinin-related gene networks that control growth and developmental processes. This integrative regulation enables plants to balance growth and stress responses under drought conditions. Melatonin acts as an important signaling molecule of stress-responsive gene networks by coordinating transcriptional reprogramming, metabolic adjustment, and hormonal signaling. This multi-layered regulation enhances plant resilience to drought stress and highlights the potential of melatonin as a powerful tool for improving stress tolerance in horticultural crops [69,77,79,82].

Table 1: Role of Melatonin in Improving Drought Resilience Among Different Plants.

Plant	Effect	Reference
Apple (*Malus domestica*)	Increased photosynthetic efficiency, larger stomatal aperture, and decreased electrolyte leakage	[83]
Chinese hickory (*Carya cathayensis*)	Better proline, soluble sugars, and ROS scavenging	[84]
Coffee (*Coffea arabica* L.)	Enhanced gas exchange, carboxylation efficiency, and root system	[85]
Cucumber (*Cucumis sativus*)	Higher photosynthetic rate, decreased MDA and H_2O_2, decreased electrolyte leakage, enhanced stomatal conductance, and increased chlorophyll content	[66]
Dove tree (*Davidia involucrata Baill*)	Activating mechanisms for glutathione metabolism and phenylpropanoid biosynthesis	[86]
Kiwi fruit (*Actinidia chinensis*)	reduced membrane damage, elevated carotenoid levels, transpiration rate, and electron transport rate	[79]
Lemon (*Lippia citriodora*)	Enhanced mineral balance, controlled ABA concentration, and improved antioxidant capacity	[87]
Salvia nemorosa L. and *Salvia reuterana Boiss*	Increased redox state, better essential oil synthesis, and higher glutathione concentration	[88]
Tomato (*Solanum lycopersicum*)	Increased GR enzyme activity and decreased lipid peroxidation	[68]

6 Modulatory Role of Melatonin in Adjustment of the Antioxidants

Drought stress induces excessive accumulation of ROS, leading to oxidative stress that disrupts cellular homeostasis and damages lipids, proteins, and nucleic acids [89]. In this context, melatonin functions as a

potent antioxidant and redox regulator, mitigating oxidative damage through both direct ROS scavenging and activation of antioxidant defense systems [37].

At the enzymatic level, melatonin enhances the activity of key antioxidant enzymes, including SOD, POD, CAT, and APX, thereby maintaining cellular redox balance under drought conditions [90]. This coordinated upregulation of antioxidant machinery enables efficient detoxification of ROS, limiting lipid peroxidation and preserving membrane integrity. Consequently, reductions in oxidative stress markers such as H_2O_2, MDA, and electrolyte leakage are consistently observed following melatonin treatment. For instance, exogenous application of melatonin significantly improved physiological performance in strawberry seedlings subjected to drought stress, including enhanced gas exchange, increased chlorophyll content, and improved growth under dehydration conditions [64]. These improvements were closely associated with reduced accumulation of H_2O_2 and MDA, indicating effective attenuation of oxidative damage (Fig. 3). Similarly, melatonin treatment has been shown to enhance the accumulation of photosynthetic pigments and soluble sugars, which contribute to osmoprotection and stabilization of cellular metabolism under stress conditions [64]. In addition to enzymatic antioxidants, melatonin also modulates non-enzymatic antioxidant systems, including ascorbic acid and phenolic compounds, which play essential roles in ROS detoxification and redox buffering. Elevated levels of these metabolites have been observed in plants treated with melatonin under drought conditions, further strengthening the antioxidant capacity and improving stress tolerance [91].

Moreover, melatonin-mediated antioxidant regulation is closely linked to its role in redox signaling, where controlled modulation of ROS levels allows their function as signaling molecules in stress-responsive pathways. This dual function balancing ROS detoxification while preserving ROS-mediated signaling enables fine-tuning of plant responses to drought stress. Collectively, melatonin acts as a central regulator of antioxidant systems by integrating enzymatic and non-enzymatic defense mechanisms with redox signaling networks. This coordinated regulation reduces oxidative damage, stabilizes cellular structures, and enhances plant resilience under drought conditions [87].

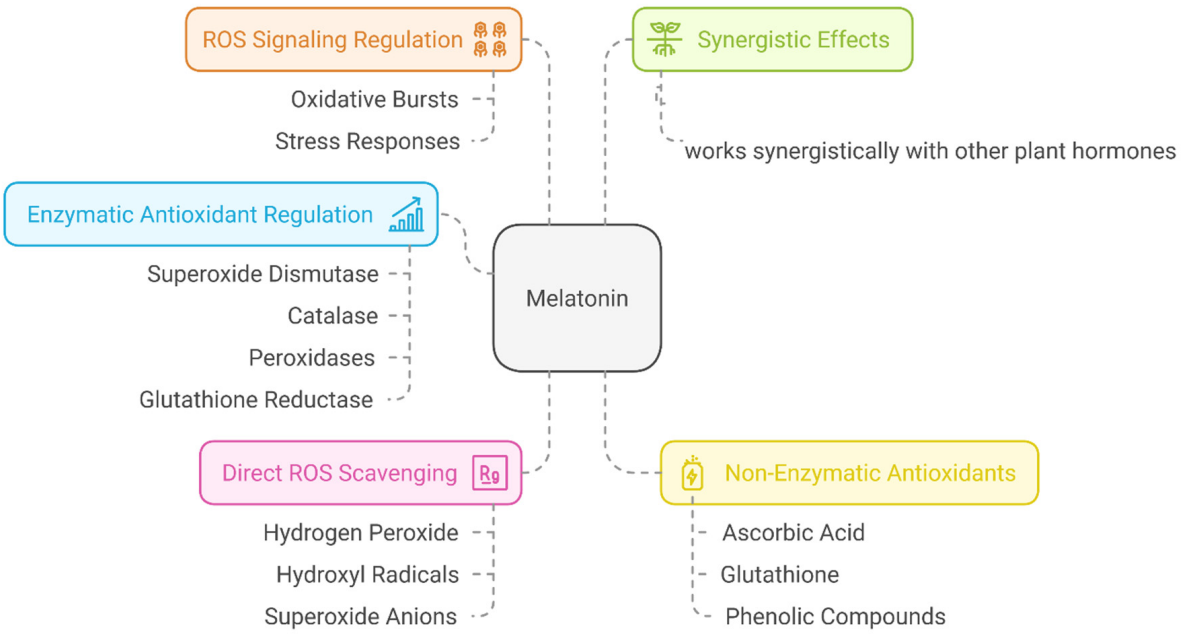

Figure 3: Role of melatonin in enhancing antioxidant defense mechanisms.

7 Modulatory Role of Melatonin in Osmolyte Regulation and Cellular Stability

Melatonin plays a critical role in osmotic adjustment and cellular stability under drought stress by regulating the accumulation of compatible solutes and maintaining ionic and membrane homeostasis. Under water-deficit conditions, plants accumulate osmolytes such as proline, glycine betaine, and soluble sugars, which function as osmoprotectants to stabilize cellular structures, preserve enzyme activity, and maintain osmotic balance [92]. Melatonin enhances the biosynthesis and accumulation of these osmolytes, thereby improving cellular hydration and sustaining metabolic activity under dehydration stress. Beyond osmolyte accumulation, melatonin acts as a priming agent that prepares plants for enhanced stress tolerance by modulating both osmotic and nitro-oxidative homeostasis. In alfalfa, melatonin treatment has been shown to improve drought resilience through coordinated regulation of osmoprotective metabolites and redox balance [57]. Similarly, foliar application of melatonin in *Capsicum* species resulted in improved growth performance and regulated ion accumulation, suggesting that melatonin enhances drought tolerance by integrating osmotic adjustment with ion homeostasis mechanisms [93].

At the cellular level, melatonin contributes to the maintenance of membrane integrity and turgor pressure by modulating ion transport systems and reducing membrane damage. It regulates the activity and expression of key ion transporters, ensuring selective uptake and compartmentalization of ions, which is essential for maintaining cellular ionic balance under stress conditions [94]. In particular, melatonin-mediated regulation of H^+-ATPase and Na^+/H^+ antiporters enhances potassium (K^+) retention while limiting sodium (Na^+) accumulation, thereby improving the K^+/Na^+ ratio and preventing ion toxicity under drought and salinity stress [17]. These regulatory mechanisms are closely associated with improved membrane stability and reduced lipid peroxidation. For example, in kiwifruit, exogenous melatonin application (50–200 μM) significantly alleviated drought-induced damage, with 100 μM identified as the optimal concentration. This treatment reduced electrolyte leakage, limited membrane injury, preserved photosynthetic pigments, and enhanced osmolyte accumulation, collectively contributing to improved stress tolerance [95].

Aquaporins are integral membrane proteins that play a central role in regulating plant water transport, cellular hydration, and overall hydraulic conductivity, particularly under drought stress conditions [96]. These water channel proteins, mainly belonging to plasma membrane intrinsic proteins (PIPs) and tonoplast intrinsic proteins (TIPs), are tightly regulated by environmental and hormonal signals to maintain water homeostasis and plant survival under water deficit [97]. Emerging evidence suggests that melatonin may contribute to drought adaptation by modulating aquaporin function indirectly through multiple regulatory pathways [98]. These include the regulation of ROS signaling, ABA-dependent pathways, and stress-responsive gene expression networks, all of which are known to influence aquaporin activity, gating, and transcriptional regulation. Through its ability to fine-tune ROS homeostasis and enhance antioxidant defenses, melatonin may help stabilize aquaporin function under oxidative stress conditions, thereby supporting sustained water transport and improving cellular water retention. Although direct molecular evidence of melatonin–aquaporin interactions in plants remains limited, current findings support a functional link between melatonin signaling and improved hydraulic efficiency under drought stress [98]. This is further supported by evidence from other biological systems, where melatonin has been shown to regulate aquaporin expression and function, suggesting a potentially conserved regulatory role across kingdoms. Therefore, aquaporins may represent a key downstream component of melatonin-mediated drought tolerance mechanisms in plants, warranting further experimental investigation.

Plant responsiveness to melatonin may also differ according to their intrinsic osmotic adjustment capacity [99]. In drought-tolerant species with efficient osmotic regulation, melatonin appears to reinforce

pre-existing protective systems, including osmolyte accumulation, antioxidant defense, and cellular water retention. Conversely, in drought-sensitive plants with limited osmotic adjustment ability, exogenous melatonin may play a compensatory role by enhancing compatible solute accumulation, membrane stability, and stress signaling pathways [100]. These species-specific differences indicate that the efficiency of melatonin-mediated protection is strongly influenced by the physiological background of the plant. Although drought and salinity stress share several physiological consequences, including osmotic imbalance, oxidative stress, and impaired photosynthesis, salinity additionally involves ion toxicity and disruption of ionic homeostasis. Melatonin has been reported to alleviate both stresses through enhancement of antioxidant defenses, osmotic adjustment, and stress-responsive signaling pathways. However, under salinity conditions, melatonin also contributes to ion homeostasis through regulation of Na^+/K^+ balance and membrane transporter activity [101]. These findings indicate that melatonin-mediated stress tolerance involves both shared and stress-specific protective mechanisms depending on the environmental constraint.

Furthermore, melatonin-mediated osmotic regulation is tightly linked to its role in maintaining cellular ultrastructure and protein stability. By promoting the synthesis of stress-responsive proteins and osmoprotective molecules, melatonin supports the stabilization of membranes, enzymes, and macromolecular complexes under dehydration stress. The resulting reduction in electrolyte leakage further reflects enhanced membrane integrity and improved cellular resilience [17]. Overall, melatonin functions as a key regulator of osmotic balance and cellular stability by integrating osmolyte biosynthesis, ion transport regulation, and membrane protection mechanisms. This coordinated response enables plants to maintain turgor, reduce cellular damage, and sustain physiological performance under drought stress conditions.

8 Influence of Melatonin on Crop Performance and Quality Maintenance

Applying melatonin under drought helps lessen the detrimental impacts on crop quality and yield [102]. Melatonin enhances reproductive development by improving pollen viability, germination capacity, and fertilization efficiency. These improvements collectively contribute to a significant yield advantage, reflected in up to a 25% increase in the number of grains per panicle, guaranteeing grain filling even during drought conditions (Table 2). Furthermore, to ensure that nutrients are allocated to reproductive tissues as efficiently as possible, melatonin controls the expression of genes implicated in food uptake and digestion, such as *NRT1.1* and *AAP1*. During drought stress, this modulation preserves grain quality and yield [103]. Moreover, melatonin application to tea seedlings significantly enhanced their drought resistance [104]. The physiological effects of melatonin may differ between C3 and C4 plants due to their distinct photosynthetic and water-use strategies [105]. In C3 species, melatonin-mediated drought tolerance is often associated with improved stomatal regulation, chlorophyll preservation, and reduced photorespiration under water deficit conditions [106]. In C4 plants generally exhibit higher intrinsic water-use efficiency and carbon fixation capacity, suggesting that melatonin may primarily enhance stress protection through maintenance of photosynthetic stability and oxidative balance [106]. These differences highlight the importance of considering plant functional type when evaluating melatonin responses under drought stress.

Table 2: Physiological and biochemical responses to drought stress across moisture deficit gradients and their modulation by melatonin.

Crop	Drought Level	Key Physiological Effects	Metabolic Changes	Hormonal Response	Effect of Melatonin	Reference
Cucumber (*Cucumis sativus*)	Field drought stress (vegetative stage)	↓ RWC, ↓ growth, ↓ photosynthesis; tolerant genotypes maintain WUE and transpiration	↑ proline, ↑ antioxidant enzymes, improved membrane stability	ABA + stress TF regulation (NAC, AP2/ERF)	Enhances osmotic adjustment and antioxidant defense	[107]
Grapevine (*Vitis vinifera*)	Deficit irrigation/drought (field conditions)	↓ stomatal conductance, ↓ photosynthesis, ↑ WUE under moderate stress	↑ phenolics, improved fruit quality under moderate drought	ABA-mediated stomatal regulation	Maintains redox balance and improves stress tolerance	[108]
Raspberry (*Rubus idaeus*)	50% irrigation + PEG-induced stress	↓ RWC (up to ~63%), altered growth depending on genotype	↑ proline, ↑ sugars, ↑ phenolics, ↑ peroxidase activity	Stress-induced metabolic signaling	Improves redox balance and osmotic regulation	[109]
Tomato (*Solanum lycopersicum*)	25%, 12.5%, 6.25% soil water content	↓ yield (~28%), ↓ fruit size, impaired mineral uptake	↑ antioxidant activity (moderate), ↓ carotenoids (severe), ↑ phenolics	Likely ↑ ABA under stress	Improves antioxidant capacity, protects pigments, stabilizes metabolism	[39]
Tomato (*Solanum lycopersicum*)	Regulated deficit irrigation	↓ photosynthesis, ↓ growth under severe deficit; improved WUE under mild stress	Altered carbon metabolism and assimilate partitioning	ABA-mediated stomatal control	Enhances WUE and photosynthetic stability	[110]

8.1 Melatonin and Auxins

Melatonin and auxins are tightly interconnected through their shared biosynthetic origin from tryptophan, establishing a metabolic and functional link between these two regulatory molecules [37]. Tryptophan serves as a common precursor for both melatonin and IAA, suggesting potential competition and coordination in their biosynthetic pathways, particularly under stress conditions. Functionally, melatonin exhibits auxin-like activity, especially in regulating root architecture and plant growth. Numerous morphological studies demonstrate that melatonin promotes root initiation, lateral root formation, and shoot growth, mimicking key physiological effects of IAA [12]. For instance, exogenous melatonin application has been shown to enhance endogenous IAA levels in drought-stressed *Moringa oleifera*, where foliar spraying (100–150 μM) significantly increased auxin content and improved growth performance [88,111]. Similarly, increased levels of IAA and indole-3-butyric acid have been reported in melatonin-treated tomato and mustard seedlings, further supporting its role in modulating auxin metabolism [112].

At the mechanistic level, melatonin regulates auxin homeostasis through multiple pathways, including modulation of auxin biosynthesis, transport, and signaling. It influences polar auxin transport by regulating the expression and activity of auxin efflux carriers, thereby affecting auxin distribution patterns within plant tissues. Interestingly, this interaction is concentration-dependent: low to moderate levels of melatonin tend to enhance auxin accumulation and transport, whereas higher concentrations (above 50 μM) may suppress IAA levels through downregulation of auxin biosynthesis- and transport-related genes [12]. This dual effect

suggests a finely tuned regulatory balance between melatonin and auxin pathways. In addition to direct effects on auxin metabolism, melatonin can regulate root development through partially auxin-independent mechanisms. Unlike IAA, melatonin does not directly activate canonical auxin-responsive gene expression or inhibit auxin degradation pathways; instead, it promotes cell division and elongation through alternative signaling routes, possibly involving ROS, Ca^{2+}, and MAPK-mediated pathways [96]. This indicates that melatonin may function as a parallel growth regulator that converges functionally with auxin signaling while maintaining distinct molecular mechanisms.

Under drought stress, the interaction between melatonin and auxin becomes particularly important for adaptive responses. Water deficit conditions typically suppress auxin-related gene expression, leading to reduced growth and impaired root development. However, melatonin treatment modulates this response by reprogramming auxin-related pathways, either enhancing or repressing specific gene sets depending on stress intensity and hormonal balance [87]. This dynamic regulation allows plants to optimize root system architecture, improving water uptake and stress resilience. The crosstalk between melatonin and auxin represents a complex regulatory network involving shared biosynthetic pathways, coordinated control of hormone homeostasis, and integration of signaling mechanisms [113]. Through this interaction, melatonin fine-tunes plant growth and developmental processes under drought stress, balancing growth promotion with stress adaptation.

8.2 Melatonin and Abscisic Acid

Abscisic acid, widely recognized as the central "stress hormone", plays a fundamental role in coordinating plant responses to drought stress by regulating physiological, developmental, and molecular processes [114]. In addition to its well-established functions in seed dormancy, germination, and vegetative growth, ABA is a key regulator of stomatal aperture and water-use efficiency, acting as a primary signal that mediates plant adaptation to water deficit [90,115]. Under drought conditions, ABA accumulates rapidly and orchestrates stress responses through transcriptional reprogramming, modulation of osmotic balance, and activation of stress-responsive genes [116]. The interaction between melatonin and ABA represents a critical regulatory module that fine-tunes drought responses through both biosynthetic and signaling pathways. ABA homeostasis is tightly controlled by the balance between its biosynthesis and catabolism, primarily regulated by key enzymes such as 9-cis-epoxycarotenoid dioxygenase (NCED) and ABA 8′-hydroxylases (CYP707A family) [117]. Melatonin modulates this balance by regulating the transcription of ABA metabolic genes, including *MdNCED3*, *MdCYP707A1*, and *MdCYP707A2*, thereby adjusting endogenous ABA levels under drought conditions [117,118].

Mechanistically, melatonin often acts as a negative regulator of ABA accumulation, leading to reduced ABA levels in drought-stressed plants [92,111]. This modulation is associated with improved physiological performance, including maintenance of chlorophyll content, delayed senescence, and enhanced stress tolerance [57]. Interestingly, despite reducing ABA levels, melatonin can still promote efficient stomatal regulation, suggesting that it enhances stomatal sensitivity and signaling efficiency rather than simply increasing ABA concentration [23]. At the signaling level, melatonin interacts with core ABA signaling components, including PYR/PYL/RCAR receptors, protein phosphatases (PP2Cs), and SNF1-related protein kinases (SnRK2s), which together form the canonical ABA signaling cascade. Melatonin has been shown to modulate the expression of these signaling genes, thereby influencing downstream transcriptional responses and stress adaptation [87]. This interaction enables melatonin to fine-tune ABA signaling outputs, balancing stress responses with growth maintenance.

A key aspect of melatonin–ABA crosstalk involves redox regulation. ABA-induced stomatal closure is closely associated with ROS signaling, particularly H_2O_2 accumulation in guard cells. Melatonin modulates this process by scavenging excess ROS while maintaining controlled ROS signaling necessary for stomatal function. This dual role allows melatonin to prevent oxidative damage while preserving ABA-dependent signaling pathways [46]. Furthermore, melatonin plays a significant role in delaying drought-induced leaf senescence by modulating ABA-responsive transcription factors, including ABF (ABA-responsive element-binding factors). By suppressing ABF-mediated transcriptional activity, melatonin reduces the expression of senescence-associated genes and limits ABA-induced aging processes [37]. This regulatory mechanism highlights the importance of melatonin in maintaining cellular integrity and prolonging photosynthetic activity under stress conditions.

Physiologically, the melatonin–ABA interaction has been validated across both drought-tolerant and drought-sensitive genotypes, such as *Malus prunifolia* and *Malus hupehensis*, where melatonin pretreatment significantly improved drought tolerance by integrating antioxidant defense, hormonal regulation, and stress signaling pathways. Additionally, exogenous melatonin application has been shown to reduce ABA accumulation, downregulate ABA-related gene expression, and enhance drought resistance by improving water status and reducing oxidative stress [37]. Together, the crosstalk between melatonin and ABA represents a dynamic regulatory network involving feedback modulation of hormone biosynthesis, fine-tuning of signaling pathways, and integration with redox homeostasis. Through this interaction, melatonin optimizes ABA-dependent stress responses while preventing excessive stress signaling, thereby enabling plants to maintain growth and enhance resilience under drought conditions.

8.3 Melatonin and Cytokinin

Recent studies have revealed a significant crosstalk between melatonin and cytokinins (CKs), highlighting their coordinated role in modulating plant responses to drought stress. Cytokinins are key regulators of cell division, chloroplast development, and delay of senescence, and their interaction with melatonin contributes to maintaining growth processes under water-limited conditions [119]. Exogenous application of melatonin has been shown to elevate endogenous CK levels, suggesting that melatonin positively regulates CK biosynthesis or signaling pathways. Conversely, cytokinins may influence melatonin biosynthesis by modulating the expression of genes involved in its production, indicating a potential bidirectional regulatory relationship between these two signaling molecules. This reciprocal interaction reflects a tightly coordinated hormonal network that integrates growth regulation with stress adaptation [120].

At the physiological level, the melatonin–cytokinin interaction contributes to the maintenance of key functional traits under drought stress, including improved relative water content, preservation of chlorophyll levels, and sustained photosynthetic efficiency [120]. These effects are largely attributed to the ability of both hormones to stabilize chloroplast structure, protect the photosynthetic apparatus, and maintain carbon assimilation under stress conditions. Evidence from creeping bentgrass, including transgenic lines overexpressing isopentenyl transferase (IPT), a key enzyme in cytokinin biosynthesis, demonstrates that elevated CK levels in combination with melatonin treatment significantly enhance drought tolerance by sustaining photochemical activity and delaying stress-induced damage [79].

A central aspect of melatonin–cytokinin crosstalk is the regulation of leaf senescence. Drought stress typically accelerates senescence through hormonal imbalance and oxidative damage; however, both melatonin and cytokinins act synergistically to delay this process. Melatonin enhances antioxidant capacity and stabilizes cellular structures, while cytokinins inhibit senescence-associated gene expression and promote chloroplast maintenance. Together, they suppress chlorophyll degradation and prolong photosynthetic

activity, thereby sustaining plant productivity under drought conditions [121]. At the molecular level, this interaction likely involves integration of cytokinin signaling components such as histidine kinase receptors, phosphotransfer proteins, and response regulators with melatonin-mediated signaling pathways, including ROS and MAPK cascades. Although the precise molecular mechanisms remain incompletely understood, emerging evidence suggests that melatonin may modulate cytokinin-responsive gene expression and signaling sensitivity, thereby fine-tuning growth-defense trade-offs under stress conditions [122]. In general, the crosstalk between melatonin and cytokinins represents a crucial regulatory module that supports plant resilience by maintaining growth, delaying senescence, and preserving photosynthetic capacity during drought stress. Further elucidation of the molecular basis of this interaction will be essential for exploiting melatonin–cytokinin networks in the development of drought-resilient horticultural crops.

8.4 Melatonin and Ethylene

Ethylene (ET) is a key phytohormone involved in regulating plant growth, stress responses, senescence, and fruit ripening. Under drought stress, ethylene production is often elevated, contributing to stress signaling but also accelerating senescence and growth inhibition. The interaction between melatonin and ethylene represents a complex regulatory module that balances stress adaptation with developmental processes [123]. In several horticultural crops, including tomato and grape, melatonin application has been shown to enhance root development, strengthen antioxidant defense systems, and modulate ethylene biosynthesis and signaling under drought conditions [124]. Notably, drought stress alone induces significant upregulation of ethylene-related genes; however, melatonin pretreatment attenuates this response, resulting in expression levels that are comparable to or lower than those of unstressed plants [92]. This suggests that melatonin prevents excessive ethylene accumulation under stress, thereby limiting ethylene-induced senescence and growth inhibition.

At the molecular level, melatonin regulates key components of ethylene biosynthesis and signaling pathways. It has been shown to upregulate *ACS4* (1-aminocyclopropane-1-carboxylate synthase), a rate-limiting enzyme in ethylene biosynthesis, as well as key signaling genes such as *NR*, *ETR4*, *EIL3*, and *ERF2*, which are involved in ethylene perception and downstream transcriptional regulation [125]. This regulation is particularly relevant during fruit development and ripening, where melatonin-induced ethylene production enhances fruit quality traits, including color development, texture, and biochemical composition. The apparent dual effect of melatonin on ethylene enhancing its biosynthesis under developmental contexts while suppressing its overaccumulation under stress highlights a context-dependent regulatory mechanism. Under drought conditions, melatonin likely fine-tunes ethylene signaling by balancing its biosynthesis with antioxidant and stress-mitigating pathways, thereby preventing premature senescence while maintaining necessary stress signaling.

Mechanistically, this interaction may involve integration with ROS signaling and MAPK cascades, where melatonin-mediated redox regulation modulates ethylene-responsive transcription factors (such as ERFs), enabling precise control of gene expression under stress conditions. This coordination ensures that ethylene signaling contributes to adaptation rather than cellular damage [113]. Taken together, the crosstalk between melatonin and ethylene represents a dynamic regulatory system that integrates stress signaling with developmental regulation. By modulating ethylene biosynthesis, perception, and downstream signaling, melatonin enhances plant resilience to drought stress while simultaneously improving fruit ripening and quality attributes.

8.5 Melatonin and Gibberellic Acids

Gibberellins (GAs) are essential phytohormones that regulate a wide range of physiological processes, including seed germination, stem elongation, leaf expansion, photosynthetic activity, stomatal regulation, and senescence control [125]. Under drought stress, endogenous GA levels are typically reduced, leading to growth inhibition, decreased biomass accumulation, and suppression of reproductive development.

Melatonin plays a crucial role in counteracting drought-induced growth suppression by modulating GA metabolism and restoring hormonal balance. Exogenous melatonin application has been shown to enhance GA biosynthesis while simultaneously reducing stress-induced inhibition of growth-related pathways, thereby improving plant performance under water deficit conditions [113]. This regulatory effect is associated with the activation of GA biosynthetic genes and the suppression of GA-deactivating pathways.

At the molecular level, melatonin influences key enzymes involved in GA metabolism, including GA 20-oxidase (GA20ox) and GA 3-oxidase (GA3ox), which are responsible for GA biosynthesis, while also modulating GA 2-oxidase (GA2ox), a key enzyme involved in GA inactivation [126]. Through this coordinated regulation, melatonin increases the pool of bioactive GAs, thereby promoting growth processes that are typically inhibited under drought stress. Although indirect interactions exist between melatonin and early tryptophan-derived metabolic pathways, melatonin primarily enhances GA accumulation through transcriptional regulation of GA metabolic genes rather than direct biosynthetic overlap [127]. This hormonal interaction has significant physiological consequences, as elevated GA levels contribute to improved cell elongation, enhanced leaf expansion, and recovery of photosynthetic capacity under drought conditions. Additionally, melatonin-mediated GA regulation supports flowering and reproductive development, which are often severely inhibited during water deficit [128,129].

From an applied perspective, melatonin priming has demonstrated significant agronomic benefits. In rapeseed, for example, melatonin treatment under drought stress resulted in improved morphological traits, increased yield components, and enhanced seed quality compared to untreated plants [130]. These effects are largely attributed to the synergistic interaction between melatonin and GA pathways, which together restore growth potential while maintaining stress tolerance. Overall, the melatonin–gibberellin interaction represents a critical growth recovery mechanism under drought stress, integrating hormonal biosynthesis regulation, transcriptional control of growth-related genes, and restoration of developmental processes. This crosstalk enables plants to balance stress adaptation with growth resumption, ensuring improved productivity under adverse environmental conditions.

8.6 Melatonin and Salicylic Acid

Salicylic acid (SA) is a multifunctional phytohormone that plays a central role in regulating plant growth, development, and stress responses, particularly in systemic acquired resistance (SAR) and adaptation to abiotic stresses [5]. Beyond its well-established role in pathogen defense, SA is also involved in modulating root development, photosynthetic performance, and hormonal crosstalk under environmental constraints.

Under abiotic stress conditions, melatonin has been reported to interact closely with SA signaling pathways, contributing to enhanced systemic acquired resistance and improved stress tolerance [131]. However, the relationship between melatonin and SA is highly context-dependent and may exhibit both synergistic and antagonistic interactions depending on species, developmental stage, and stress intensity. For instance, in onion, exogenous SA application under stress conditions was found to negatively affect endogenous melatonin levels, suggesting possible feedback regulation or metabolic competition between the two signaling molecules [132].

Despite this complexity, numerous studies have demonstrated strong synergistic effects between melatonin and SA in enhancing drought tolerance. In rapeseed (canola), combined seed priming with melatonin and foliar SA application resulted in pronounced improvements in growth performance, yield components, water content, and osmotic potential, accompanied by elevated endogenous levels of both hormones [133]. At the molecular level, melatonin and SA co-regulate a wide range of drought-responsive genes, including those involved in antioxidant defense, osmotic adjustment, and stress signaling pathways [134]. This coordinated regulation leads to enhanced expression and activity of key antioxidant enzymes, improved redox homeostasis, and reduced accumulation of reactive oxygen and nitrogen species under drought stress.

Mechanistically, the melatonin–SA interaction integrates ROS signaling, MAPK cascades, and transcriptional reprogramming, enabling fine-tuned regulation of both local and systemic stress responses. This interaction also strengthens photosynthetic efficiency by protecting chloroplast structure and maintaining pigment stability under water deficit conditions [135]. Collectively, the crosstalk between melatonin and salicylic acid represents a critical regulatory module that integrates immune signaling with abiotic stress adaptation. Through coordinated control of redox balance, gene expression, and physiological protection mechanisms, melatonin and SA synergistically enhance plant drought tolerance and improve overall performance under adverse environmental conditions.

9 Exogenous Application of Melatonin Enhances Drought Tolerance

Exogenous melatonin application has emerged as an effective strategy to enhance drought tolerance, including a wide range of fruits and vegetables such as tomato (*Solanum lycopersicum*), apple (*Malus domestica*), grape, kiwifruit (*Actinidia chinensis*), pepper (*Capsicum annuum*), citrus, and several leafy and seed vegetables [79,87,136–138]. Across these species, melatonin consistently improves plant performance under water-deficit conditions by enhancing physiological resilience and stabilizing growth–yield relationships. At the physiological level, melatonin significantly improves photosynthetic efficiency in fruits and vegetables by preserving chlorophyll content, protecting photosystem II (PSII), and maintaining thylakoid membrane integrity under drought stress. In tomato and apple, melatonin enhances gas exchange parameters, increases net photosynthesis, and sustains ATP synthase activity, thereby preventing drought-induced collapse of carbon assimilation [136]. Similarly, in kiwifruit and pepper, melatonin improves light energy utilization and stomatal regulation, leading to improved water-use efficiency and sustained growth under limited water availability [79,137].

A major mechanism underlying melatonin-induced drought tolerance is the strengthening of antioxidant defense systems. In tomato, alfalfa, maize, and pepper, exogenous melatonin enhances the activity of enzymatic antioxidants (SOD, CAT, POD, APX), while also increasing non-enzymatic antioxidants such as phenolics and flavonoids. This dual antioxidant reinforcement reduces ROS accumulation, limits lipid peroxidation, and protects cellular membranes from drought-induced oxidative damage [138–141]. As a result, fruit and vegetable tissues maintain better cellular integrity, delayed senescence, and improved post-stress recovery capacity.

In addition to oxidative protection, melatonin regulates osmotic adjustment in plant species by promoting the accumulation of compatible solutes such as proline, soluble sugars, and glycine betaine. This osmolyte accumulation enhances cellular water retention, stabilizes proteins and membranes, and maintains turgor pressure under dehydration stress. In tomato, pepper, and alfalfa, this osmotic regulation is directly associated with improved leaf water status and sustained physiological activity under drought conditions [137,138,141]. At the molecular level, melatonin modulates key drought-responsive genes involved in photosynthesis, antioxidant metabolism, hormone signaling, and secondary metabolite biosynthesis.

Melatonin downregulates senescence-associated genes while enhancing chloroplast stability and photosynthetic gene expression, thereby delaying drought-induced leaf aging and maintaining productivity. In pepper, melatonin activates nitrogen metabolism genes and flavonoid biosynthesis pathways, strengthening metabolic adaptation and enhancing stress tolerance [137].

Melatonin also plays a crucial role in root system architecture. Melatonin enhances root length, lateral root formation, and root hair development, thereby improving water uptake efficiency under drought stress [16]. This improved root plasticity is essential for maintaining water balance in fruit and vegetable crops exposed to intermittent or prolonged drought conditions. Importantly, melatonin interacts with key phytohormones, including ABA, auxins, and cytokinins, to fine-tune growth–stress balance. In soybean, melatonin reduces drought-induced ABA accumulation while maintaining hormonal equilibrium, leading to improved stomatal regulation, delayed senescence, and sustained fruit and vegetable quality [142]. In general, exogenous melatonin acts as a multifunctional biostimulant in fruits and vegetables by integrating photosynthetic protection, antioxidant defense, osmotic regulation, hormonal crosstalk, and gene expression reprogramming. These coordinated effects ultimately improve yield stability, fruit quality, and stress resilience under drought conditions. However, most studies remain restricted to controlled environments, emphasizing the need for field-based validation and optimization of application strategies to ensure practical agricultural implementation in plant production systems.

10 Conclusion and Future Prospects

Melatonin has emerged as a key regulatory hub in enhancing plant tolerance to drought stress, one of the most significant constraints on global agricultural productivity. Rather than functioning solely as a protective molecule, melatonin acts as a regulatory molecule within interconnected hormonal networks that coordinates multiple phytohormonal pathways, including cytokinins, ethylene, gibberellins, salicylic acid, and other stress-related hormones. Through this extensive hormonal crosstalk, melatonin modulates essential physiological processes such as photosynthetic efficiency, root system architecture, chlorophyll stability, antioxidant defense activation, osmotic regulation, and stress-responsive gene expression. These integrated responses enable plants to maintain growth–defense balance and improve adaptation to water-limited environments. Although abscisic acid has long been considered the central regulator of drought responses, accumulating evidence suggests that melatonin functions as a regulatory element in stress signaling pathways. However, the underlying molecular mechanisms governing melatonin-mediated hormonal interactions remain incompletely understood, particularly at the levels of receptor signaling, transcriptional regulation, ion transport processes, and post-translational modifications. In addition, emerging evidence pointing to melatonin-derived metabolites such as N-nitrosomelatonin suggests that melatonin signaling may involve additional regulatory layers that are still largely unexplored.

Future research should prioritize moving from descriptive and omics-based observations toward mechanistic and causality-driven approaches. In particular, there is a critical need for functional validation studies to confirm the roles of candidate genes and pathways identified through high-throughput analyses. Such approaches should include gene knockout and overexpression systems, CRISPR/Cas-based functional validation, ion channel and transporter activity assays, aquaporin functionality measurements, ROS quantification, and controlled drought physiology experiments. These methods are essential to establish direct causal links between melatonin signaling and drought adaptive traits. From an applied perspective, translational strategies offer promising opportunities for enhancing crop drought resilience. Advanced technologies such as nanocarrier-based delivery systems, precision priming approaches, and genome editing tools may enable targeted manipulation of melatonin biosynthesis and signaling pathways. Optimization

of application parameters, including dosage, timing, and delivery methods, will be essential to ensure reproducibility and field-level effectiveness across diverse environmental conditions. In the context of climate change and increasing water scarcity, melatonin represents a promising natural biostimulant and central regulatory molecule for sustainable agriculture. Harnessing melatonin-mediated signaling networks provides a robust framework for improving crop resilience, stabilizing yield performance, and supporting future food security under increasingly variable climatic conditions.

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