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Review

Role of Melatonin in Directing Plant Physiology

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Abstract: Melatonin (MT), a naturally occurring compound, is found in various species worldwide. In 1958, it was first identified in the pineal gland of dairy cows. MT is an "old friend" but a "new compound" for plant biology. It brings experts and research minds from the broad field of plant sciences due to its considerable influence on plant systems. The MT production process in plants and animals is distinct, where it has been expressed explicitly in chloroplasts and mitochondria in plants. Tryptophan acts as the precursor for the formation of phyto-melatonin, along with intermediates including tryptamine, serotonin, *N*-acetyl serotonin, and 5-methoxy tryptamine. It plays a vital role in growth phases such as the seed germination and seedling growth of crop plants. MT significantly impacts the gas exchange, thereby improving physio-chemical functions in plant systems. During stress, the excessive generation and accumulation of reactive oxygen species (ROS) causes protein oxidation, lipid peroxidation, nucleic acid damage, and enzyme inhibition. Because it directly acts as an antioxidant compound, it awakens the plant antioxidant defense system during stress and reduces the production of ROS, which results in decreasing cellular oxidative damage. MT can enhance plant growth and development in response to various abiotic stresses such as drought, salinity, high temperature, flooding, and heavy metals by regulating the antioxidant mechanism of plants. However, these reactions differ significantly from crop to crop and are based on the level and kind of stress. The role of MT in the physiological functions of plants towards plant growth and development, tolerance towards various abiotic stresses, and approaches for enhancing the endogenous MT in plant systems are broadly reviewed and it is suggested that MT is a steering compound in directing major physiological functions of plants under the changing climate in future.

Keywords: melatonin; indolamine; abiotic stress; antioxidant; plant growth

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1. Introduction

MT (*N*-acetyl-5-methoxy-tryptamine) is a naturally occurring compound in various species. In 1958, it was identified in the pineal gland of dairy cows [1]. MT is an "old friend" but a "new compound" for plant biology. MT was first identified in higher plants as reported by Dubbels et al. [2], Van Tassel et al. [3], and Hattori et al. [4]. MT has drawn a lot of study interest since it was discovered and found in plants in 1995. It has been detected and measured in more than 140 plant species in recent years [5,6]. It is a versatile compound that is extensively distributed in a variety of plant organs, including the roots, stems, leaves, fruits, and seeds. Different plant tissues contain significantly varied amounts of MT. Blask and his co-workers proposed the term "phytomelatonin" in 2004, referring to its plant-based source [7]. Tryptophan, a type of indoleamine, is the starting molecule for MT like that of auxin and ought to be involved in the control of growth and development. It has physiological impacts on plants, which include stimulating seedling growth, formation of primary roots, lateral and adventitious roots, and modifying the branching and growth cycles of leaves and stems, and also resists against leaf senescence by enhancing photosynthesis, stimulating flowering and seed development [8]. MT also takes part in several cellular processes in the name of antioxidant and free radical scavenging [9]. Additionally, MT has been linked to improved seed sprouting, maturation, photosynthesis, biomass production, circadian rhythm, redox network, membrane integrity, root development, leaf senescence, osmoregulation, and resistance to environmental stresses like salt, drought, heat, oxidative stress, and heavy metals. MT levels in plants are noticeably higher when exposed to a various stressors, including salt, drought, temperatures, UV radiation, metal pollution, and pathogenic infections, implicating that MT plays a role in plant stress tolerance [10]. It functions as an antioxidant and contributes to controlling ROS and nitrogen species (RNS) in plants because of its pleiotropic qualities. It is more efficient than glutathione and vitamin E at regulating a number of antioxidant enzymes, including glutathione reductase, catalase (CAT), peroxidase (POX), and superoxide dismutase (SOD). It boosts the mitochondria's electron transport chain's effectiveness, thereby reducing electron leakage. Because MT functions as a signaling molecule connected to defense systems against diverse biotic and abiotic threats, it is regarded as a master plant regulator that supports plant development and growth [11]. The signaling molecules in MT biosynthesis in plants under stress are yet to be clearly identified [12]. Employing MT as a bio-stimulator for the sustained production of crops without damaging the surrounding environment could, therefore, be of utmost relevance.

MT was found to increase the secondary metabolites like fatty acid and alkaloid content in different crops like coffee and soybean under various abiotic stresses [13], but the mechanism behind this has to be investigated. MT helps in stomatal closure at night to avoid water loss in arid regions by regulating ROS signaling through its receptor PMTR1 and maintaining homeostasis [14]. External application of a low concentration of MT was found to enhance seed germination, lateral root growth, and photosynthesis under various abiotic stresses [13]. Application of MT increased salt stress tolerance in rice, melon, and grapevine [15,16]; drought stress tolerance in corn and apple [17,18]; heat stress tolerance in Arabidopsis [19]; cold stress tolerance in corn and cucumber [20,21]; and heavy metal stress tolerance in wheat, tomato, Arabidopsis, and rice [22–25].

The study of MT action in plants is quickly expanding due to its phenotypic hormone effect on plant growth systems. It examines the crucial function of MT in regulating plant growth and development as well as its potential physiological mechanism for reducing abiotic stressors on plants. This review will contribute to a detailed knowledge of the current state of plant MT research and help us to understand MT's role in directing plant physiology more meticulously, and we may speculate that plant MT research will go on a new path in the future.

2. Biosynthesis of Melatonin in Plants

The MT production process in plants and animals is distinct. Many elements, including light, have a vital role in controlling its production in plants. MT is specifically expressed in chloroplasts and mitochondria in plants. Tryptophan acts as the precursor for the formation of phyto-melatonin, along with intermediates including tryptamine, serotonin, *N*-acetyl serotonin, and 5-methoxy tryptamine (Figure 1). According to the report from Tan and Reiter [26], the intermediates of MT production are found in several sub-cellular compartments including the cytoplasm, mitochondria, endoplasmic reticulum and chloroplasts.

Tryptophan decarboxylase (TDC) first decarboxylates tryptophan to produce tryptamine in the cytoplasm, tryptamine-5-hydroxylase (T5H), and then performs an enzymatic hydroxylation to produce serotonin in the endoplasmic reticulum. *N*-acetyltransferase (SNAT) and acetyl serotonin methyl transferase (ASMT) convert serotonin through acetylation and methylation reactions into *N*-acetyl serotonin in chloroplasts and 5-methoxytryptamine in the cytoplasm. *N*-acetyl serotonin produced in chloroplast reacts with the ASMT in the cytoplasm and transforms into MT; meanwhile, 5-methoxytryptamine produced in cytoplasm moves into the chloroplast and reacts with SNAT to synthesize MT [27]. Alternatively, an enzyme known as caffeic acid O-methyltransferase (COMT), which regulates several substrates, can also convert *N*-acetyl serotonin into MT in a different route that has been studied through plants. COMT can also transform serotonin into 5-methoxytryptamine and produce MT through SNAT catalyzation [28].

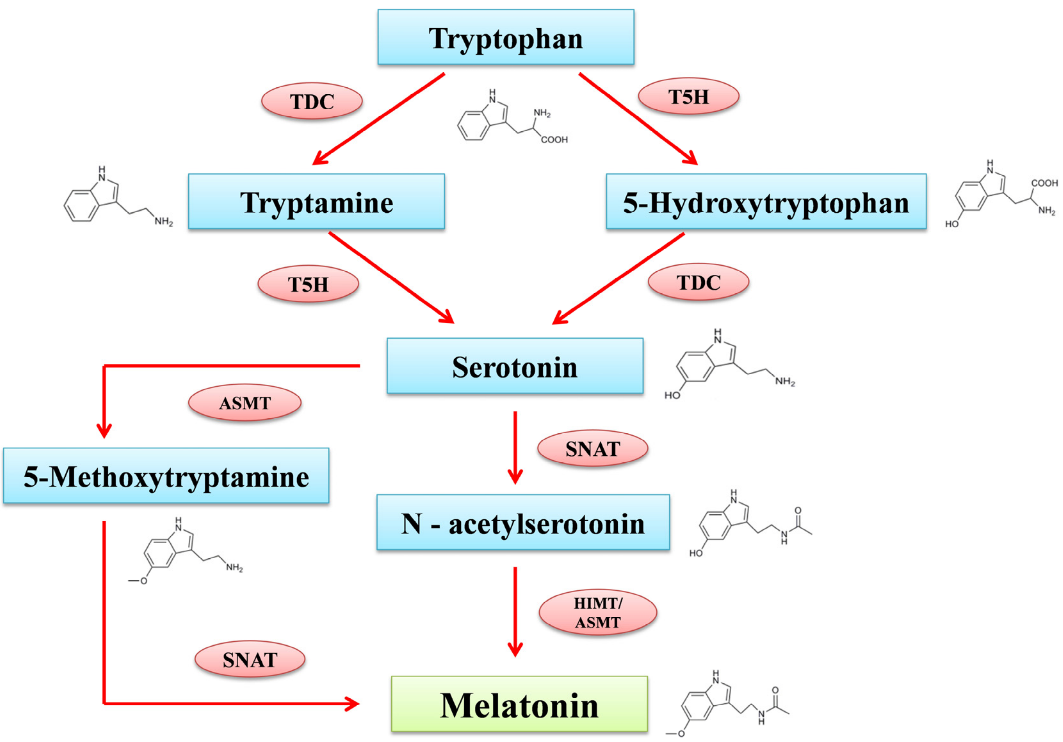

Figure 1. MT biosynthesis pathway in plant system. TDC: Tryptophan decarboxylase; T5H: tryptamine 5-hydroxylase; SNAT: serotonin-*N*-acetyltransferase; ASMT: N-aceylserotonin methyltransferase; COMT: caffeic acid *O*-methyltransferase.

3. Melatonin's Role in Plant Growth and Physiology

3.1. Germination

In the life cycle of higher plants, seed germination is a complicated process governed by several coordinated metabolic, cellular, and molecular activities. It is also a crucial time for the establishment of crop populations. Germination involves a number of metabolic and physical processes. This stage, which is similarly susceptible to stress and critical for determining whether plants will survive under adverse conditions, is greatly influenced by the external environment. According to Li et al. [29], MT functions as a signaling molecule and positively controls the germination process in *Cucumis melo* by upregulating the genes for gibberellin (GA) biosynthesis (*CsGA20ox* and *CsGA3ox*) and abscisic acid (ABA) catabolism (*CsCYP707A1* and *CsCYP707A2*). A similar finding was also reported by Chen et al. [30] in cotton. Abiotic stress, such as stress like elevated temperature, lowers the cotton seeds' ability to germinate, which leads to poor germination and crop stand which lends support to the findings of Snider et al. [31]. According to Lei et al. [32], application of MT improved seed germination and reserve mobilization in wheat under chromium stress.

Raza et al. [33] revealed that exogenous MT promotes the activity of several antioxidant enzymes, which decreased the formation of ROS and enhanced the viability of seedlings under elevated temperatures. Application of MT in *Lupinus albus* potentially stimulated the vegetative growth in cotyledons and etiolated seedlings [34]. Similarly, in red cabbage (*Brassica oleracea rubrum*), exogenous MT promotes seed germination [35]. Previous studies have proven that pretreatment with MT can improve the seed germination of the various crops like green gram [36], rice [37], tomato [38], maize [39], *Medicago sativa* [40], *Triticale hexaploide* [41], and cotton [42]; also, it acts as a signaling molecule for the upregulation of genes involved in the biosynthesis of gibberellin (GA) that might be responsible for seed germination in cucumber [43]. Based on the result derived from Castañares and Bouzo [16], the germination percentage of the melon decreased drastically with increased Ec (electrical conductivity) of the water solution. However, the 6 h seed pretreatment with MT significantly increased the germination percentage. Findings of Rajora et al. [44] also revealed that under varied abiotic stress situations, priming seeds with MT enhances and speeds up the seed germination process. To speed up the germination process, seed priming changes the physiology of the embryo and activates hydrolytic enzymes [45].

3.2. Shoot and Root Growth

Due to the buildup of ABA, which further inactivates cell-wall-loosening enzymes under water stress in wheat, shifting the apoplastic pH from acidic to alkaline restricts the development of the plant's shoots and roots [46]. The process of cell elongation involves an indoleamine molecule [47]. Pretreatment with MT results in a drop in intercellular pH to an acidic state and activates the enzymes responsible for loosening cell walls, which in turn triggers cell elongation like IAA [48]. As a consequence, seed priming with MT enhanced seed germination and seedling development through synthesizing stress-related proteins and activating signaling pathways in rice under stressful conditions [49]. Ahmad et al. [50] stated that MT along with the application of nitrogen significantly improved the shoot fresh and dry biomass in maize seedlings. Exogenous MT enhances the accumulation of soluble sugars and the protein level, which regulates osmotic adjustment under stressful conditions in cotton [51]. The application of MT stimulates the production of endogenous growth-inducing substances like metabolites, phytohormones, and increasing ROS and RNS scavenging systems in plants [52] which might lead to the production of higher shoots and denser roots. The fact that MT also causes the auxin-related genes to become active suggests that the auxin signal pathway is necessary for MT-mediated root development [53]. Ahmad et al. [54] described that increased shoot and root length, leaf area, and biomass accumulation after MT treatment improve the maize plant's ability to withstand salt stress. Additionally, MT treatment boosted the amount of other endogenous growth induce factors as IAA, which led to the development of a denser root system [55]. A similar effect was found in other crops like rice [37], wheat [56], tomato [57], tobacco [58], and soybean [59] revealing that the growth and establishment of seedlings from seeds that had been pretreated with MT was favorable. Sultana and Barthakur [60] explored that seed priming with MT elicits positive effects on wheat root traits such as length, volume, and surface area of the seedling.

3.3. Gas Exchange

Photosynthesis is the most important physiological function found in all green plants that is severely affected by abiotic stresses [61]. Abdulbaki et al. [62] explained that abiotic stresses reduce the production of assimilatory powers (ATP and NADPH) and Rubisco activity by destroying the chloroplast grana structure and photosynthetic electron transport system. The reduced diffusion and concentration of intercellular CO_2 in the carboxylation site of rubisco also decreases the photosynthetic rate under stress [63]. Chlorophyll is a key photosynthetic pigment found in all higher plants and plays a vital function in absorption of light energy. Fu et al. [64] reported that the metabolite concentrations of chlorophyll a, chlorophyll b, and carotenoids were decreased under heat stress in wheat. The enhanced activity of chlorophyll-degrading enzymes like chlorophyllase, pheophytinase, and chlorophyll-degrading peroxidase catalyze the breakdown of chlorophyll molecules in response to stress [65]. Wang et al. [66] suggested that a direct link was observed between MT and the concentration of photosynthetic pigment in soybean. MT reduces the rate of chlorophyll degradation by lowering the transcript levels of pheophorbide-a-oxygenase (*PAO*) which is involved in chlorophyll metabolism [67]. The expressions of genes such as *Chlase*, *PPH*, and *Chl-PRX* associated with degradation of chlorophyll biosynthesis were downregulated by MT in *Agrostis stolonifera* [68]. Shi et al. [69] stated that MT increases the Bermuda grass photosynthetic pathway by protecting the chlorophyll molecule from degradation and enhances the expression of photosynthetic proteins like LHCa and PsaG during oxidative stress. MT also protects the chloroplast ultrastructure from oxidative damage and recovers photosynthetic accessory pigments like carotenoids, chlorophyll b, xanthophyll, and anthocyanin from stress [70]. Liu et al. [67] suggested that application of MT decreases the expression level and its relative mRNA abundance of genes involved in senescence (*SAG12*) and the programmed cell death process. MT slows down the aging process of leaves by enhancing the ROS scavenging mechanism, which stabilizes the chloroplast structure and protects photosynthesis-related genes from deterioration [71] in the tomato plant.

Stomata play a vital role in the regulation of photosynthesis, transpiration rate, and water status of the plant [72]. MT regulates the opening of stomata through upregulation of the ABA catabolism process and simultaneously downregulates ABA anabolism that results in reduced accumulation of the endogenous ABA level. The decreased ABA level by MT reduces the production of H_2O_2 in guard cells of stomata that makes the stomata remain open and maintains the water status of the plant [73]. Leaf water status and leaf temperature are positively regulated by transpiration rate. The increased transpiration rate by MT enables the plant to maintain a lower leaf temperature, thereby improving photosynthetic efficiency [74]. The positive effect of MT on transpiration rate and stomatal conductance through the regulation of ABA level was also noticed in tomato [75], rice [76], and pepper [77].

Farooq et al. [78] observed the positive effect of MT on the photochemical efficiency (Fv/Fm) of the photosystem (PSII) in *Brassica napus*. Raza et al. [33] opined that stress induces excessive production of ROS which results in the peroxidation of lipid membranes and denaturation of proteins essential for chlorophyll biosynthesis that subsequently decreases the photosynthetic efficiency in plants. MT enhances the quantum yield of PSII by preventing photooxidative damage and assisting in the repair of photo-oxidatively damaged D1 protein [79]. The increase in the efficiency of PSII (Fv/Fm) is mainly attributed to the better functioning of PS II that has a higher number of reaction centers and improved photosynthetic electron transport rate (ETR) [57].

3.4. Antioxidant or ROS Scavenging

The crops are more vulnerable to the several abiotic stresses with changing climate during their growth phases. During stress conditions, plants convert 1–2% of the consumed oxygen into reactive oxygen species, specifically, hydroxyl radical ($^{\bullet}OH$), hydrogen peroxide (H_2O_2), superoxide radical ($O_2^{\bullet-}$), and singlet oxygen ($^1O_2$). Stress enhances the production of ROS that results in cellular oxidative damage. The excessive generation and accumulation of ROS causes protein oxidation, lipid peroxidation, nucleic acid damage, enzyme inhibition, early leaf senescence, and necrosis [80]. Plants produced various enzymatic, such as CAT, POX, APX, SOD, GPX, and GR, and non-enzymatic antioxidants, like vitamins, carotenoids, stilbenes, and flavonoids, to capture the excess ROS in the plant system and thereby protect the plants from oxidative stress. Currently, MT is an inevitable compound present in the plant system and functions as a powerful antioxidant using both direct and indirect mechanisms during abiotic stress conditions. MT scavenges free radicals produced under stressful circumstances by increasing the endogenous antioxidants such as ascorbic acid and glutathione [58]. The expression level of genes related to antioxidant enzyme activity like SOD, CAT, APX, and GPX was also increased by MT in response to stress [81]. Kaur et al. [82] noticed that the Asada-Halliwell pathway, a crucial antioxidant enzymatic cycle, was regulated by MT in order to enhance the ROS scavenging mechanisms in stressed plants. Zhang et al. [83] suggested that MT stimulates the activity of H_2O_2 scavenging enzymes such as CAT, POD, and APX as well as ABA-degrading enzymes. Furthermore, MT controls the AsA-GSH cycle, which is essential for ROS detoxification, and enzymes like APX, MDHAR, DHAR, and GR were involved in the regulation of this cycle [84]. Rehman et al. [85] explained that MT effectively scavenges ROS by increasing the activity of the antioxidant enzyme glutathione peroxidase (GPX), which scavenges lipid peroxides, hydroperoxides, and H_2O_2 under stress.

MT possesses amphiphilic characteristics that enable it to diffuse and distribute readily across lipid membranes and the cytoplasm. The MT-bound hydrophilic side of the lipid bilayer prevented lipid peroxidation by directly neutralizing the damaging chemicals produced under stressful circumstances [86]. Lei et al. [87] opined that application of MT to rapeseed minimizes the free radical formation and generation of ROS like H_2O_2 and O_2^{-}. The integrity of the plant cell membrane was improved by MT through the increased activity of antioxidant enzymes like SOD, CAT, APX, and GPX [88]. MT reduces the effects of oxidative stress by directly scavenging ROS through enhanced antioxidant enzyme activity that ultimately reduces the MDA level in plants [89]. The increased antioxidant enzyme activity and defense system by the exogenous application of MT under stress conditions were also reported in wheat [90], tomato [91], cabbage [92], and rice [93]. The generation of superoxide anion radicals is inhibited by MT via limiting the level of O_2 flux under stress conditions when ADP levels are higher [94]. MT functions through several methods as a mediator in many antioxidant pathways, such as the glutathione ascorbate cycle, peroxidases, superoxide dismutase, and CAT under abiotic stress responses in plants [95]. Talaat and Todorova et al. [96] also observed that the plants treated with MT have increased ascorbate (AsA) and reduced glutathione (GSH) content, thereby reducing the formation of H_2O_2 in plant cells. The increased non-enzymatic antioxidants like AsA and GSH production are thought to be crucial for maintaining the ROS balance in plants under stress. The positive role of MT on antioxidant enzyme activity was also reported by Ye et al. [97] and Yan et al. [98] in barley and tomato.

4. Melatonin's Role in Secondary Metabolites' Expression

Abiotic stress downregulates the accumulation and concentration of plant metabolites, whereas foliar application of MT positively upregulates the metabolites in the plant system. At the cellular level, the concentration of several metabolites was altered by the exogenous application of MT that was both directly or indirectly involved in plant tolerance against drought stress in green gram, and the expressed metabolites were involved in the intermediates of different metabolic pathways [99] (Figure 2). Xie et al. [100] reported that the metabolites involved in the carbon metabolic pathway which includes glycolysis, the oxidative pentose phosphate pathway and the tricarboxylic acid (TCA) cycle, were upregulated by MT and showed a direct link between the carbon metabolic pathway and MT in rice. Proline is one of the compatible solutes that accumulates in plant cells in response to cadmium stress and increases the osmotic adjustment in order to retain membrane integrity. In addition, the experiment found that exogenous application of MT could significantly improve the metabolite group such as amino acids, sugar, and sugar alcohols in tomato plant [91] and the compounds were assigned as intermediates for plant metabolic pathways. Sheikhalipour et al. [101] showed that increased proline concentration by MT also increases the stabilization of protein structures from denaturation under moisture stress. Saddhe et al. [102] described that metabolites like proline and some sugars such as glucose, fructose, sucrose, and trehalose were involved in the regulation of osmotic adjustment under osmotic stress. MT increased the transcription level of various sucrose-related enzymes like sucrose synthase, invertase, phosphatase, and fructokinase and sucrose transporters in plant cells [103]. Yang et al. [104] explained the importance of

MT between *MdFRK2* and plant growth and *MdFRK2* was found to be involved in the MT-mediated accumulation of sugars like glucose, fructose, and sucrose in apple leaves. Jiang et al. [105] found that high levels of metabolite concentration related to amino acids were observed in MT treatment that results in enhanced physiological activities. The primary function of glycolysis in the plant metabolic pathway is to supply energy in the form of ATP and synthesize precursors essential for metabolism of fatty acids and amino acids [106]. Zhang et al. [107] stated that MT improves the metabolites engaged in carbohydrate and amino acid metabolism and upregulates the glycolysis pathway in plants. MT enhances plants' tolerance to abiotic stresses through detoxification of ROS and osmotic adjustment by synthesizing and accumulating secondary metabolites such as phenols, ascorbic acid, and carbohydrates such as mannitol and ribose which play a major role in antioxidants and osmolytes [108]. Foliar application of MT during drought stress expressed multifaceted metabolites in *Carya cathayensis* which facilitates the upregulation of biosynthetic pathways such as ABC transporters, porphyrin and chlorophyll metabolism, carotenoid biosynthesis, carbon fixation and metabolism, sugar metabolism, and the phenylpropanoid pathway in MT-treated plants [109]. For plants to fight against various environmental stresses, MT regulates the stress signaling pathways through the accumulation of various flavonoids, polyamines, and phenolic compounds in the plant system [110].

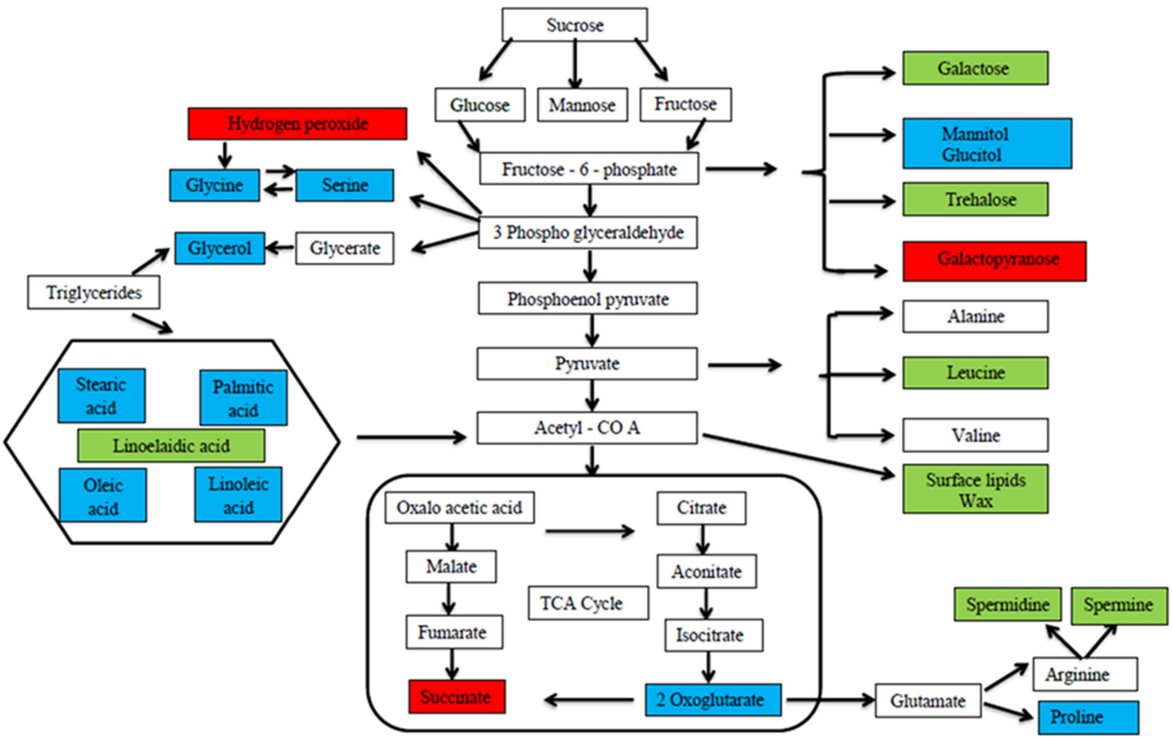

Figure 2. Different metabolite expressions in control and MT-treated green gram plant under drought stress. In the figure, the blue color highlighted box shows the metabolite expressions in both control and MT-treated plants, the green color highlighted box shows the metabolite expression in MT-treated plants alone, and the red color highlighted box shows the metabolite expression in control plants [99].

The GC-MS metabolomic study of the investigation showed that more than 50 compounds were expressed and regulated by MT treatment in cassava plants [111]. These compounds include amino acids (glycine, arginine, and thymine), fatty acids (oleic acid, palmitic acid, streaic acid, linoleic acid, linolenic acid, and traumatic acid), antioxidants (coumarins, phenols, and flavonoids), aromatic compounds (piperidine), and digitoxin. Salt-stressed plants without MT treatment also expressed some compounds in minimum amounts such as gamolenic acid, gelsimine, burnamicine, oxalic acid, and melibiose, whereas traumatic acid, glycine, arginine, oleic acid, arginine, thymine, and phenols were some compounds found only in MT-treated plants and not in salt-stressed plants. MT application was responsible for the synthesis of spermidine, spermine, and putrescine bioactive compounds through activating precursors like arginine and ornithine [89]. The various abiotic stress studies found that MT endorses the secondary metabolites like spermidine, spermine, and putrescine in *Cucumis sativus*; flavones, flavanone, luteolin, and isoflavone in pigeon pea [95,112]; and rosmarinic acid, luteolin flavone, and apigenin flavone in *Dracocephalum kotschyi* Boiss [113].

5. Melatonin's Role in Crop Yield and Quality

MT enhances the growth-related attributes as well as the photosynthetic pigments and thus maximizes the photoassimilate production and translocation efficiency from source to sink tissues and finally the yield [114]. Khan et al. [115] mentioned that in tomato plant, the number of fruits per plant, fruit yield, and quality characters (ascorbic acid, lycopene content, and β carotene) were increased in MT-treated plants. Hassan et al. [116] reported that exogenous MT significantly improves the weight of the bunch, hands per bunches, total weight of hands, and finger length in banana. In addition, Hu et al. [84] also stated that increased photosynthetic carbon metabolism and partitioning efficiency in the MT-treated plants enhanced the boll formation and seed yield in cotton. MT regulates a variety of physiological and biochemical processes in plants, thereby improving the net photosynthetic rate and productivity of the crop [117]. Medina-Santamarina et al. [118] explained that MT showed a positive effect on the improvement of sink strength that ultimately results in improved berry size, weight, and yield of pomegranate. MT enhances the seed filling rate, seed weight, and final yield of maize crop by regulating the hormonal balance [50]. Jiang et al. [105] also observed that MT delays the early leaf senescence process and improves the photosynthetic efficiency by minimizing the production of ROS, which shows a direct impact on the improvement of quality and yield of rice grains. Liu et al. [67] reported that the number of fruits per plant, per fruit weight, and yield per plant were significantly improved in MT-treated cucumber plants. Application of MT showed a positive correlation between photosynthetic rate, antioxidant enzymes, and seed yield in soybean [119] and maize [120].

Mohamed et al. [121] observed an improvement in oil quality of rapeseed cultivars due to the priming of *Brassica napus* L. seeds with MT, which increased the concentration of unsaturated fatty acids like linolenic and oleic acids with reduced glucosinolates and saturated fatty acids such as palmitic and arachidic acids under salinity stress. The application of MT improved yield-related characteristics such as seed yield per plant, 1000 seed weight, seed oil content, and seed yield in mustard [122]. Wang et al. [123] investigated the impact of MT on yield traits of soybean and reported an increased number of pods, seeds per pod, and grain yield under stress. In cucumber, the number of fruits, fruit weight, and total yield of the plant were increased under osmotic stress in response to MT treatment [124]. Pretreatment of MT improved the number of pods, seed number per pod, total seed weight, and seed yield of soybean under salt stress [125]. Debnath et al. (2018) found that exogenous application of MT improved the quality and yield of tomato fruits exposed to abiotic stress. Liu et al. [47] noticed that the priming of seeds with MT improved the fruit quality of tomato with the increased accumulation of lycopene, ascorbic acid, and mineral elements in fruits.

Ibrahim et al. [126] observed an enhanced fruit quality in tomato due to MT application which improved the antioxidant enzymes, lycopene, ascorbic acid, and total soluble solids. Gurjar et al. [127] found that exogenous MT increased the shelf life of fruits and vegetables. Medina-Santamarina et al. [118] described that the quality parameters of pomegranate fruits like fruit size, color, total acidity, total soluble solids, fruit number per tree, and fruit yield were improved by the application of MT. Nasser et al. [128] observed that the increase in transcriptome alterations during the ripening process in grape berries enhanced the quality of berries due to MT treatment. Under drought stress, foliar application of MT enhanced the yield and quality of *Moringa oleifera* L. in terms of amino acid composition, glutamic acid, and nutrition such as nitrogen, phosphorus, potassium, calcium, and magnesium [129]. In flax, total phenolic content, TSS, proline, and free amino acid contents of the seeds were increased by exogenous MT treatment [130]. Farouk and Al-Amri [131] reported that the application of MT in rosemary plants improved the essential oil content and yield under stress conditions. Foliar spray of MT in medicinal lemon verbena shrub (*Lippia citriodora*) enhanced the yield and essential oil content by 52% and 32%, respectively, under stress conditions [132].

6. Melatonin's Role in Abiotic Stress Mitigation

Plants experience many adverse situations throughout their lifespan. In order to survive and reproduce successfully in adverse conditions such as drought, salinity, high temperature, flooding, and heavy metal stress, plants have evolved a variety of response mechanisms. MT is a universal compound participating in the nullification of the various abiotic stress responses as a pleiotropic signaling molecule. Furthermore, it is a proficient scavenger of RNS as well as ROS. Numerous research studies have been carried out to investigate the activities of MT in plants since its discovery, indicating its protective properties against abiotic stressors (Table 1).

Drought and high temperature stress reduce the permeability of water in the plants [133]. Stomata play a vital role in regulation of photosynthesis, transpiration rate, and plant water status in response to abiotic stresses [134]. Rao et al. [135] opined that ABA acts as a key mediator for the closure of stomata under stress conditions, which ultimately affects a cascade of physiological and molecular processes. Wang et al. [136] explained that exogenous MT ameliorates the oxidative stress and improves transpiration rate and stomatal conductance in sweet corn. The increase in transpiration rate and stomatal conductance might be due to the upregulation of the ABA catabolism process and the simultaneous downregulation of ABA anabolism that results in reduced accumulation of the endogenous ABA level; this fact was already reported by Hu et al. [137]. The decreased ABA level reduces the production of H_2O_2 in guard cells of stomata that makes the stomata remain open and maintains the water status of the plant under stress [29]. This might be the reason for the increased transpiration rate and stomatal conductance in green gram under water deficit and high temperature stress conditions. Jiang et al. [138] reported that MT improves the stomatal conductance by regulating the ROS-mediated stomatal closure that results in a higher transpiration rate in response to stress. Leaf water status and leaf temperature are positively regulated by transpiration rate. The increased transpiration rate by MT enables the plant to maintain lower leaf temperatures, thereby improving photosynthetic efficiency [139]. Supriya et al. [140] found that an increased stomatal conductance in MT-treated plants regulates the canopy temperature by enhancing the water loss which ultimately results in lower water use efficiency under stress. At the single-leaf level, the water use efficiency is governed by stomatal conductance and transpiration rate [136]. The response of water use efficiency is closely linked with physiological processes by regulating the concentration of CO_2 and H_2O in plant cells [27]. MT maintains better water use efficiency under stress through the control of stomatal movements; therefore, it improves the net photosynthetic rate as reported by Li et al. [141]. The positive effects of MT on transpiration rate and stomatal conductance through regulation of the ABA level were also noticed in tomato [142], rice [143], and barley [144].

6.1. Drought

Plants grown in water-stressed environments confront numerous biochemical and molecular challenges, resulting in reduced plant development [145]. Drought stress reduces photosynthesis by interfering with the mechanism of light harvesting and utilization, significantly altering the metabolism of photosynthetic pigments, resulting in a decrease in RuBisCo function and disruption of the photosynthetic apparatus [146] in finger millet [36]. MT helps plants to restore the photosynthetic efficiency by protecting the system from the harmful impacts of drought [147]. It reduces chlorophyll degradation during drought conditions and enhances photosynthesis, transpiration, and stomatal conductivity [148]. MT increases the photosynthetic rate by improving the photochemical efficiency (Fv/Fm) of photosystem II (PSII) and the rate of electron transport (ETR) [149]. After MT treatment, leaves have a higher relative water content, which favors the protection of chloroplast structures in maize [150]. It also helps to maintain cell turgor, which increases the capacity of stomatal openings and conductance [147]. This enhanced stomatal conductance promotes the passage of water and CO_2, which in turn promotes photosynthesis in MT-treated plants [151].

Furthermore, it has been shown that MT upregulates the transcript levels of genes involved in ABA breakdown (*MdCYP707A1* and *MdCYP707A1*) while it downregulates *MdNCED3*, a crucial gene in the ABA biosynthesis pathway. This cellular reaction was aided by an antioxidative mechanism and efficient H_2O_2 scavenging. Both these strategies are thought to work synergistically to improve stomatal function [152]. MT boosts the capacity of plants to scavenge ROS, protecting them from the damaging effects of drought-induced oxidative stress. This enhanced ROS scavenging is brought on by the MT-stimulated antioxidative defense system in plants developing under drought [153]. MT regulates the drought-induced synthesis of superoxide anions in plant cells, either by increasing scavenging or by limiting the creation of superoxide anions [154]. MT also improves H_2O_2 scavenging efficiency in plants growing in drought conditions [18]. This is followed by the increased detoxification of damaging hydroxyl radicals that contribute to oxidative stress induction [155]. MT also affects the ascorbate-glutathione cycle and causes ROS, such as H_2O_2, to be scavenged directly [156].

MT-mediated efficient ROS scavenging in drought-stressed plants protects plant cell walls. This is substantiated by lower MDA levels and less electrolyte leakage in MT-treated plants under water-stress circumstances (Figure 3). MT stimulates the activity of ABA-degrading enzymes as well as H_2O_2 scavenging enzymes such as CAT, APX, and POD in drought-stressed crops [18]. MT boosts cuticular wax formation and enhances deposition on the leaf's surface, resulting in little water loss. This increased production is attributed to increased transcript levels of genes that encode enzymes implicated in wax biosynthetic pathways, like KCS1 (ketoacyl-CoA synthase 1) and LTP1 (lipid transfer protein 1) [157].

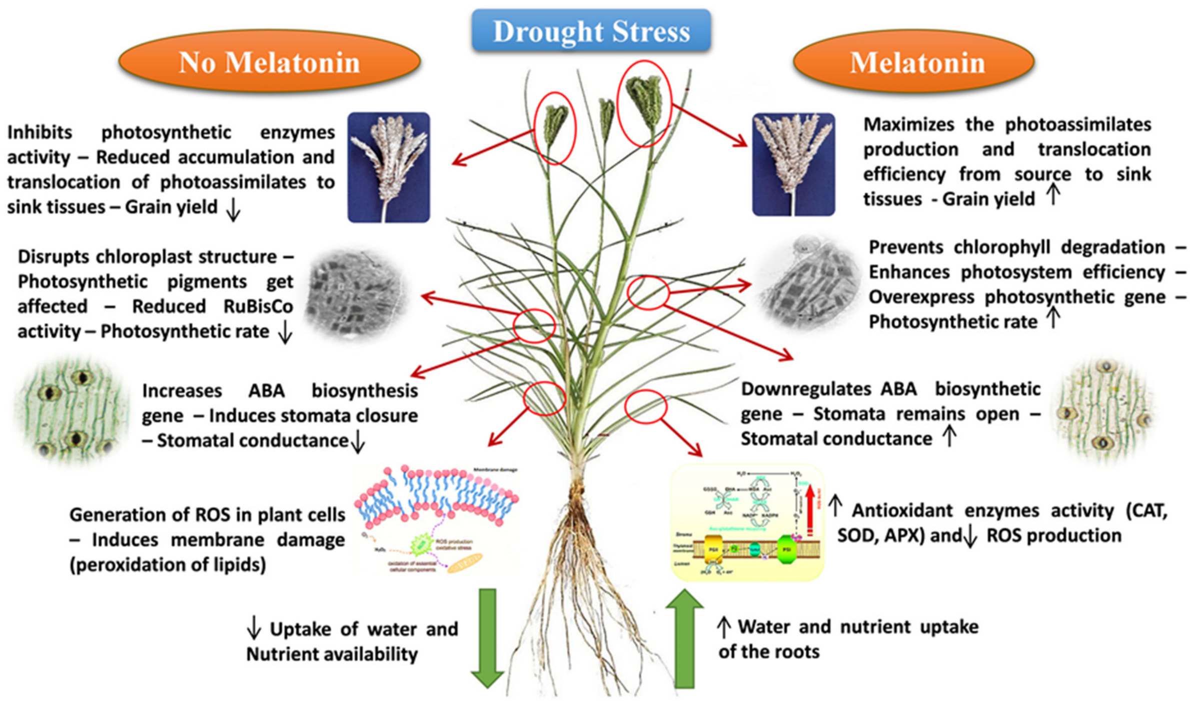

Figure 3. Melatonin effects on finger millet under drought stress (source: Anitha [158]).

6.2. Salinity

According to Kesawat et al. [159], plants under salt stress are more likely to produce too many ROS, which can lead to membrane lipid or protein peroxidation and the death of normal plant cells. When salt concentrations are excessive, plant roots experience osmotic stress and have lower water potential. Additionally, the absorption of nutrients and water is impacted, which hinders plant growth and development and causes wilting and plant mortality [160]. Under stressful situations, the concentration of MT in the leaves and roots of grapevine seedlings is raised considerably, and the rise is amplified by the severity of stress [161]. To prevent water loss during salt stress, plants seal their stomata. This lowers stomatal conductance (GS), which in turn lowers photosynthesis [162]. However, when subjected to salt stress, employing the right amount of MT may improve stomatal function and enable plants to reopen their stomata [163]. Furthermore, under salt stress, MT increased photosynthesis-related gene transcription while preserving the photosynthetic apparatus [69].

By enhancing chlorophyll formation and reducing its breakdown during salt stress, MT treatment improved the total chlorophyll content and the maximum photochemical reaction efficiency of PSII (Fv/Fm). Under very salty conditions, plants transport extra salt ions from the cytoplasm inside the vacuole or compartmentalize them into separate tissues [164]. The salt-induced Na+/H+ antiporter in the tonoplast oversees compartmentalizing ions within the cytoplasm into vacuoles in order to reduce ion concentrations within the cytoplasm [165]. MT is essential for maintaining ion homeostasis; in order to maintain ion homeostasis under salt stress, MT specifically upregulates the transporter genes *NHX1* and *AKT1* [166]. The application of MT as a set treatment combined with foliar spray resulted in higher photosynthetic rate, stomatal conductance, transpiration rate, osmotic potential, osmatic adjustment, proline, and soluble protein content of cassava plants under salt stress [167].

6.3. Temperature

One of the main factors limiting plant growth is heat stress, which has a significant negative impact on agricultural production worldwide. In order to sustain numerous physiological, biochemical, and molecular mechanisms to deal with heat stress conditions, MT works as a plant growth regulator. In a recent study, scientists discovered that the ability of tomato to absorb CO_2 and produce photosynthetic pigment increased when 100 M of MT was applied. MT lowers photoinhibition and defends the PSI and PSII reaction centers [168]. By enhancing antioxidant defense systems like the bate-glutathione cycle and rewiring the metabolic pathways for nitric oxide production and PAs, MT reduced the severity of heat stress damage [169]. MT enhances tea quality under heat stress by encouraging photosynthetic and biomass accumulation in tea plants [170]. In addition, MT-treated seedlings showed increased expression of anti-stress responsive genes like *TaMYB80*, *TaWRKY26*, and *TaWRKY39* as well as ROS-related genes *TaCAT*, *TaPOD*, and *TaSOD* [90]. MT treatment increases the root length; leaf area; plant height; fresh and dry root weight; shoot weight; CAT, SOD, POD, and APX activities; soluble sugar content; and protein content of maize [120] and mung bean [73] (Figure 4) under stressful conditions.

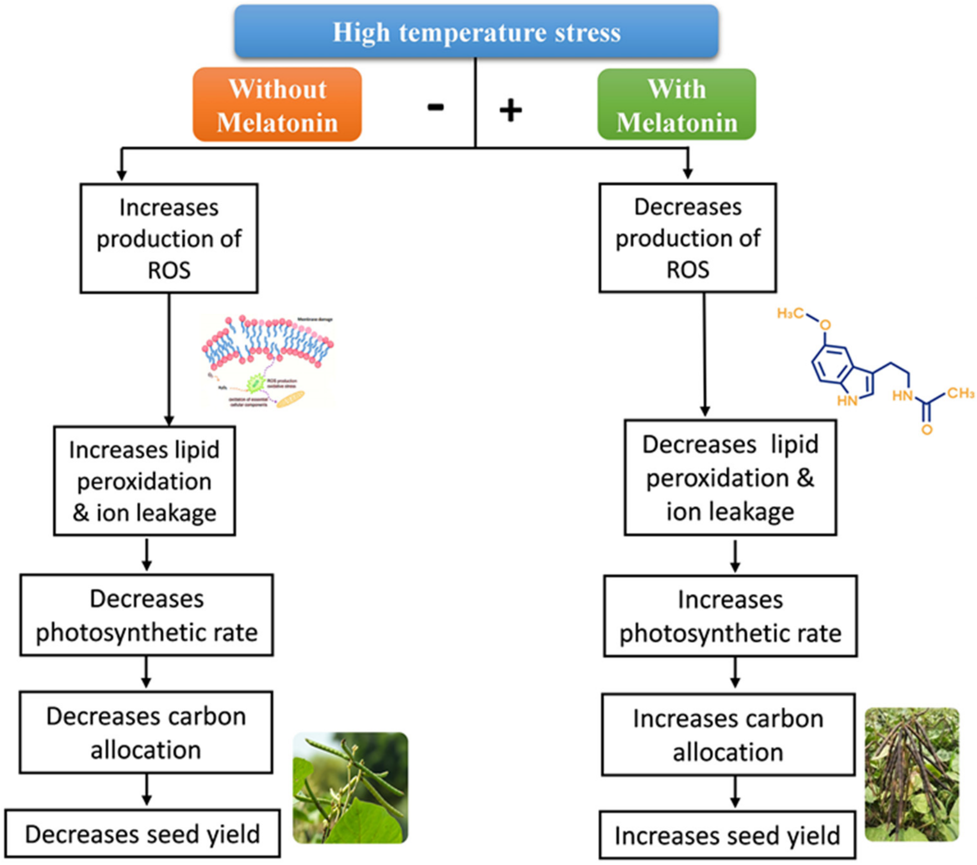

Figure 4. Schematic representation of melatonin-mediated high−temperature stress tolerance in plants. (Source: Modified from Kuppusamy et al. [73].)

6.4. Flooding

MT has been shown to be an effective phytohormone for protecting apple plants against waterlogging stress as reported by [171]. A recent research study by [172] examined the effects of MT pretreatment on lucerne under waterlogging stress and found that it could mitigate the damage caused by the stress and improve chlorophyll content, plant growth, and PSII efficiency. Zheng et al. [171] originally suggested that MT facilitated the mechanism for tolerating waterlogging in apple seedlings by successfully preventing the ROS burst and subsequent mitochondrial breakdown; this mechanism preserves aerobic respiration and photosynthesis. Another concept in lucerne was proposed by [172] via interacting with or directly controlling the metabolic pathways of ethylene and polyamines (PAs). The scientists suggested that MT promotes waterlogging tolerance, at least in part, by regulating ethylene and polyamine's production because ethylene is suppressed and polyamine is promoted. As a result, cell membranes are more stable, photosynthesis is improved, and there is less ethylene-responsive senescence [172].

6.5. Heavy Metals

Toxicity caused by heavy metals (HM) is one of the most harmful abiotic stressors. Plants do not need lead [31], cadmium [173], mercury (Hg), or arsenic (As), all of which are extremely detrimental to plants [174,175]. Authors including *Chandrakar* et al. [176], Chen et al. [177], and Umapathi et al. [91] reported that the majority of heavy metals continuously produce ROS which can lead to oxidative stress in plants and the unanticipated side effect of heavy metal toxicity (Figure 5). Lipid peroxidation, a harmful condition brought on by HM-induced ROS, impairs the integrity and functionality of cell membranes [178,179]. Numerous studies emphasized how heavy metals affect the accumulation of endogenous MT in plants. Studies revealed that HMs induced endogenous MT biosynthesis in the root tissue of *Hordeum vulgare* (barley), *Solanum lycopersicum* (tomato), and *Lupinus albus* (lupin) [34,180,181]; in the leaves of *Nicotiana tabacum*, *Arabidopsis thaliana*, and tomato [182,183]; and in the seedlings of *Oryza sativa* (rice) [184]. The structural integrity of cellular organelles such as chloroplasts, mitochondria, and the endoplasmic reticulum is dramatically compromised in HMs under Cd stress, for example. Endogenous serotonin *N*-acetyltransferase (SNAT) enzymes are subsequently released into the cytosol as a result [185,186] where they can easily come into contact with serotonin, resulting in *N*-acetyl serotonin synthesis and ultimately MT formation.

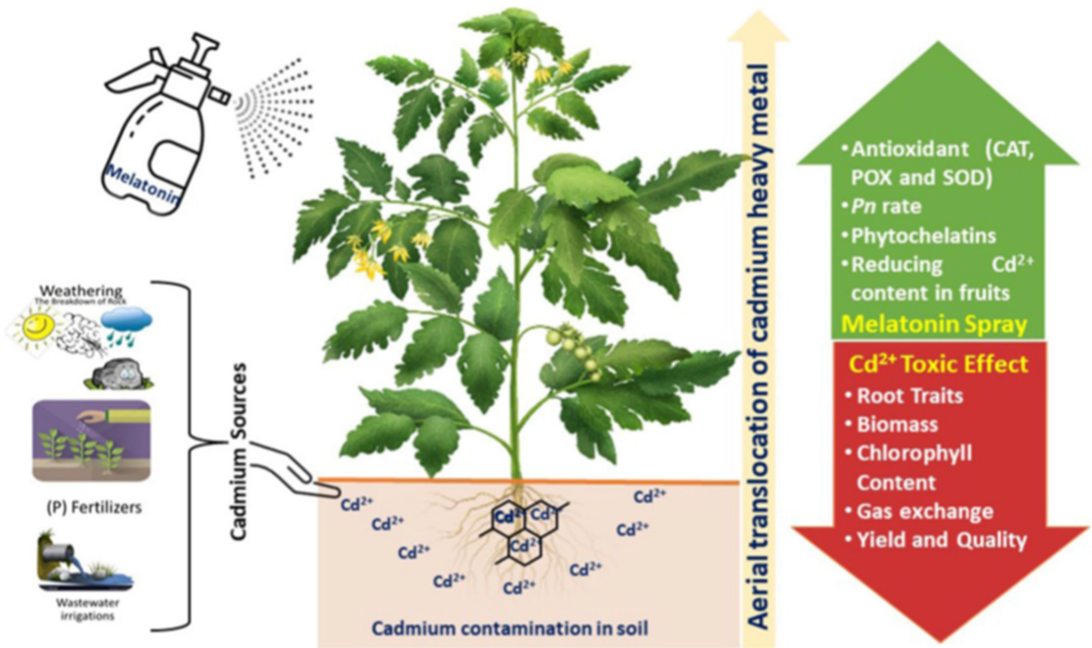

Figure 5. Overview of melatonin mitigating Cd toxicity in tomato plant (source: Umapathi et al. [91]).

MT is useful for a variety of purposes, and because of its capacity to directly neutralize ROS, it aids in protecting plants from oxidative stress. Additionally, it possesses chelating properties, which may help to lessen the toxicity brought on by such metals. MT, an amphiphilic molecule, may easily diffuse through cell membranes, enter the cytoplasm, and go to subcellular compartments [187]. Through the activation of antioxidant defense mechanisms, exogenous MT application can reduce Cd and Zn damages and enhance tolerance in lemon balm plants as opined by Hodzic et al. [188].

Table 1. Effect of melatonin on the physiological functions in crop plants under various abiotic stresses.

S.No.	Plant Species	Abiotic Stress	Melatonin Concentration (μM)	Plant Response	Reference
1	Rice	Salinity	20	Improve the root and shoot, dry weight, and K^+ content	[15]
		Drought	200	Improve the germination percentage and seedling characters	[37]
		High temperature	200	Improved photosynthesis, stabilize starch synthesis, and reduce grain chalkiness	[189]
		Low temperature	150	Improved seed germination and traits associated with germination	[190]

Table 1. *Cont.*

S.No.	Plant Species	Abiotic Stress	Melatonin Concentration (µM)	Plant Response	Reference
2	Wheat	Salinity	200	Seed germination and seedling characteristics	[56]
3	Maize	Drought	100	Effective increase in the antioxidant enzyme and photosystems activity Reduces the H_2O_2, superoxide anion, and MDA levels	[191]
4	Cotton	Drought	100	Delaying leaf senescence	[192]
5	Soybean	Nitrogen deficient	100	Better total nitrogen fixation capacity and upregulating the expression of genes related to nitrogen metabolism (*NR2*, *NiR*, *GS1β*, *GOGAT*, and *GmAAP6a*)	[66]
6	Green gram	High temperature	100	Improve the root and shoot length Reduced the MDA content and improve the antioxidant content	[193]
		Drought	100	Increased seed germination and seedling vigor	[36]
7	Finger millet	Drought	60 as nano formulation	Increased photosynthetic activity, effective antioxidant system, and improved carbohydrate assimilation and translocation	[194]
			40 and 60	Improve the seed germination and seedling establishment	[195]
8	Tomato	Cadmium stress	108	Minimizing the Cd accumulation in fruit and increase the antioxidant enzyme activity	[91]
		High temperature	10	Silencing the *COMT1*gene and increase the APX and CAT activity	[196]
9	Cassava	Salinity	430	Higher gas exchange and soluble protein content	[167]
10	Alfalfa	Salinity	300	Increase the antioxidant capacity, osmotic regulation, and photosynthesis	[72]
11	Apple	Salinity	0.1	Maintain ion homeostasis, enhance the level of antioxidant enzymes, and maintain photosynthesis	[166]
		Drought	100	Improved nitrogen assimilation and endogenous MT content	[148]
12	Grapes	Drought	100	Prevent chloroplast damage and improve antioxidant activity	[197]
13	Coffee	Drought	300	Enhanced carboxylation efficiency and antioxidant activity	[153]

Table 1. *Cont.*

S.No.	Plant Species	Abiotic Stress	Melatonin Concentration (μM)	Plant Response	Reference
14	Tea	Chilling stress	100	Prevent oxidative damage and improved photosynthetic pigments	[198]
		Drought	100	Reduce membrane damage and enhance the level of proline, total protein, and sugars	[199]
		Cd Toxicity	150	Scavenge reactive oxygen species and enhance the level of antioxidants	[200]
15	Cucumber	Chilling stress	200	Reduce electrolyte leakage and improve photosynthesis	[201]
16	Melon	Chilling stress	200	Reduce ROS and increase proline and soluble protein content	[202]
17	Peach	Chilling stress	200	Prevent oxidative damage and improve the ascorbic acid content in fruits	[203]

7. Approaches for Enhancing Endogenous Melatonin

MT is a pivotal compound present in the plant system. In that way, increasing endogenous MT is crucial to combat against abiotic stresses in the agricultural field. MT biosynthesis consists of four enzymatic processes, viz., TDC, T5H, SNAT, and ASMT.

The transgenic approach is a useful tool for improving the endogenous MT content. Nonetheless, notable studies were conducted concerning the overexpression of MT under various abiotic stresses in different crops. Previously, studies confirmed that abiotic stress significantly increases the MT level in plant systems [204,205]. In order to boost the synthesis of antioxidants like MT without impairing plant growth and development or having unintended side effects on other metabolic pathways, endogenous metabolic pathways must be modulated. Overexpression of genes and enzymes involved in MT biosynthesis through the transgenic approach might improve the endogenous MT. In plants, the major enzymes involved in the MT biosynthetic pathway such as serotonin *N*-acetyl transferase (*SNAT*) and *N*-acetyl serotonin methyl transferase (*ASMT*) were found to have maximum catalytic efficiency values at 55 °C (Byeon et al., 2014). *N*-acetyl serotonin O-methyltransferase (*ASMT*), one of the enzymes involved in the MT biosynthesis process, has been expressed in transgenic plants [206]. In transgenic tomato plants, the overexpression of MT biosynthetic genes such as arylalkyl amine *N*-acetyl transferase (*AANAT*) and hydroxyindole-O-methyl transferase (*HIOMT*) increases the endogenous MT level and enhances the tolerance capacity of plants against stresses [207]. The enzyme caffeine acid methyltransferase (*COMT*), which is involved in MT biosynthesis, may also help to control plant development, growth, and stress responses. *CrCOMT* from *Carex iridescent* overexpression alters MT production in *Arabidopsis thaliana* and causes an increase in salt stress [208]. In Brassica rapa, *miR168a* enhances the MT level through increased expression of the *O-METHYLTRANSFERASE 1* (*OMT1*) gene, which is responsible for MT biosynthesis [209].

The serotonin *N*-acetyltransferase (*SNAT*) enzyme which is crucial for MT biosynthesis increases the accumulation of MT in plants in response to stress conditions [210]. Overexpression of the *VvSNAT1* gene also increased MT synthesis in transgenic Arabidopsis [211]. Suppression of the *OsSNAT* gene reduced the levels of endogenous MT in transgenic rice (*Oryza sativa* L.) plants, which results in poor seedling growth and development [182]. In transgenic Arabidopsis plants, mutation of the apple *MzSNAT5* gene leads to the reduced production of MT in the mitochondria, which results in enhanced ROS accumulation and susceptibility of plants to drought stress [186]. Increased MT synthesis was observed in transgenic Arabidopsis by overexpression of the *TaCOMT* gene [104]. The tolerance capacity of the tomato plant to salinity stress improved with the upregulation of MT biosynthetic gene *SlCOMT1* [212]. Similarly, overexpressing the *HIOMT* gene in apple resulted in increased MT synthesis and reduced production of ROS [213].

Exogenous application is another approach to bring up the endogenous MT content inside the plant. In addition to being a natural bioregulator, exogenous compounds like benzothiadiazole (BTH) and chitosan (CHT) can be used to stimulate the production of MT in plants [214]. Numerous studies were conducted on the enhancement of endogenous MT through exogenous application in various plants such as tomato [183], Arabidopsis [215], groundnut [216], and hemp [217]. In response to various stresses in plants, the application of MT accumulates more endogenous MT by overexpressing the MT biosynthetic genes such as *TDC*, *T5H*, *SNAT*, and *ASMT* [27]. In addition, the foliar spray application of MT significantly enhanced the endogenous MT content in the tomato plant under cadmium-induced heavy metal stress [183].

8. Conclusions

Crop abiotic stress causes a significant yield decline, which has an impact on the safety of the world's food supply. Therefore, it is more important to concentrate on raising agricultural plants' resistance to stress. Globally, MT is evolving as a pioneer compound to mitigate the abiotic stresses in the agricultural field. We outlined the regulatory systems that underpin plants' ability to withstand abiotic stress in this review. MT significantly improves the scavenging of ROS and RNS to enhance the antioxidant capacity. The biosynthetic pathway of MT has been identified in a number of plant species in which TDC, T5H, SNAT, ASMT, and COMT are the key enzymes for MT biosynthesis. Due to its positive impacts on plant tolerance to environmental stressors, the MT catabolic pathway and its metabolites have drawn more and more attention in recent years. The exogenous MT application in varied crops exhibited a better performance in physiological and biochemical traits associated with improved yield potential. Moreover, the exogenous application of MT is not specific to genotype and it is less time-consuming, more cost-effective, and is readily available for large-scale applications. The effect of MT on growth, physiology, yield, and biochemical parameters reveals that there might be a long-term effect of this compound in improving the abiotic stress tolerance. Hence, it is necessary to study how the pretreatment of MT could be effective to prepare crops for unpredicted sudden stress conditions. Some of the methods through which MT interacts with other phytohormones remain obscure, despite the fact that it can affect the manufacturing and signaling of other phytohormones. MT application studies have been extensively studied only at a laboratory level and the large-scale commercial application of MT has been rarely conducted. Hence, field-level examinations are required to assess the effects of MT on crop yield under open conditions.

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