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Review

# Melatonin: A Vital Pro-Tectant for Crops against Heat Stress: Mechanisms and Prospects

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**Abstract:** Heat stress (HS) is a serious environmental stress that negatively affects crop growth and productivity across the globe. The recent increase in atmospheric temperature caused by global warming has increased its intensity, which is a serious challenge that needs to be addressed. Plant growth and development involves a series of physiological, metabolic, and biochemical processes that are negatively affected by heat-induced oxidative stress, disorganization of cellular membranes and disturbed plant water relations, nutrient uptake, photosynthetic efficiency, and antioxidant activities. Plant tolerance to abiotic stresses can be substantially increased by the application of bio-stimulants, without posing a threat to the ecosystem. Melatonin (MT) is a multi-functional signaling molecule that has the potential to protect plants from the adverse impacts of HS. MT protects the cellular membranes, maintains the leaf water content, and improves the water use efficiency (WUE) and nutrient homeostasis; thereby, improving plant growth and development under HS. Moreover, MT also improves gene expression, crosstalk of hormones, and osmolytes, and reduces the accumulation of reactive oxygen species (ROS) by triggering the antioxidant defense system, which provides better resistance to HS. High endogenous MT increases genes expression and antioxidant activities to confer HS tolerance. Thus, it is important to understand the detailed mechanisms of both exogenous and endogenous MT, to induce HS tolerance in plants. This review highlights the versatile functions of MT in various plant responses, to improve HS tolerance. Moreover, we also discussed the MT crosstalk with other hormones, antioxidant potential of MT, and success stories of engineering MT to improve HS tolerance in plants. Additionally, we also identified various research gaps that need to be filled in future research using this important signaling molecule. Thus, this review will help the readers to learn more about MT under changing climatic conditions and will provide knowledge to develop heat tolerance in crops.

**Keywords:** antioxidant defense; genes expression; heat stress; melatonin; photosynthesis; reactive oxygen species

## 1. Introduction

The global climate is drastically changing, and this is significantly affecting crop productivity [1]. Extreme weather events, particularly rising temperatures and inconsistent rainfall, pose a serious threat to the successful cultivation of crops, to meet the needs of an ever-mushrooming population [2]. Heat stress (HS) is a serious issue, owing to the rise in global temperature, and it significantly affects the plant growth, development, and productivity of field crops [2,3]. The continuous rise in global temperature owing to anthropogenic activities is a serious worry for mankind and will significantly affect crop productivity and food security in coming years [3,4]. HS significantly disrupts plant photosynthetic efficiency, owing to the production of reactive oxygen species (ROS) [5], which also cause damage to major molecules, including proteins, lipids, and DNA [2,6–11]. ROS also adversely affects the membrane integrity and enzymatic activities, and resultantly alters growth and development and causes yield losses [12–18]. HS also alters the carbohydrate metabolism in plants by changing the expression of genes involved in this metabolism [19]. Moreover, high temperature shortens the time needed for anthesis and grain filling and reduces pollen fertility, the development of pollen tube grains, seed setting, and grain weight; therefore, resulting in a significant loss in final productivity [20–23]. HS also denatures proteins and enzymes, and reduces nutrient and water uptake, which is also a major reason for the reduction in plant growth under HS [2]. Plants possess an excellent antioxidant defense system to cope with the damaging effects of heat-induced ROS [2,4]. Additionally, plants also accumulate various osmolytes (proline, glyciene-betaine), soluble sugars (fructans, mannitol, and raffinose trehalose), and hormones to counter the effects of HS [2]. Plants with a higher accumulation of sugar and hormones show better tolerance against abiotic stresses [19].

Melatonin (MT) is an important hormone that plays a significant role in plant growth and development, under a wide range of abiotic stresses. MT is an important signaling molecule that maintains plant physiological functioning and protects the plants from different abiotic stresses [24–28]. MT works as an important molecule to scavenge ROS [29], and it also protects the photosynthetic apparatus from oxidative stress and improves plant photosynthetic efficiency [25,30]. MT regulates the opening of the stomatal and improves the synthesis of chlorophyll, RuBisCo activity, and efficiency of the photosystem (PS-I and PS-11); thereby, improving plant photosynthetic performance under HS stress [25,31]. MT also improves the activities of the antioxidant system, maintains membrane stability, plant water relations, and enhances HS tolerance in wheat [32] and tomato [33,34]. It also increases the expression of stress responsive genes that support the photosynthetic machinery and increase the tolerance against HS [32].

MT is also involved in different processes, ranging from growth to fruit ripening, leaf senescence, and mitigation of stress-induced oxidative damage [25,35]. It also shows interaction with different signaling molecules and hormones, to counter the effects of abiotic stresses [31,36–39]. Additionally, MT also reduces ROS, cell damage, and electrolyte leakage, and resultantly improves plant growth and biomass production under stress conditions [39,40]. Recently, the role of MT in plants grown under HS has been well explored. Therefore, in this review, we systematically presented the different mechanisms of MT-induced HS tolerance in plants. Moreover, we also discussed the MT-mediated antioxidant system and engineering of MT biosynthesis to improve the HS tolerance in plants. Additionally, we also provided detail about MT crosstalk with different osmolytes and hormones and future research directions, to demonstrate its importance for HS tolerance in plants. Thus, this review will provide new insights to readers about the role of MT in plants under HS. This information will be of great significance to develop cultivars with improved MT synthesis, for better heat tolerance.

## 2. Plant Responses to Heat Stress

Plants are sessile organisms exposed to different abiotic stress that negatively affect their growth and development. HS is a serious abiotic stress that has deleterious impacts on plants during their life cycle (Table 1). Seed germination is the first stage of any plant, and HS significantly reduces seed germination by restricting water and nutrient availability and disrupting the enzymatic activities [41,42]. HS also reduces the root length and leads to poor seedling growth and stand establishment; therefore, causing significant yield losses [43,44]. Moreover, HS also reduces cell numbers, cell size, growth, and biomass production [45,46] and induces diverse morphological changes in plants, including stem and leaf burning, leaf scorching, fruit discoloration, leaf rolling, senescence, abscission, chlorosis, and necrosis [47,48].

**Table 1.** Effects of different heat stress levels on the growth, physiology, and yield of different crops.

| Crop Species | Heat Stress | Stage of HS | Major Effects | Reference |
|---|---|---|---|---|
| Rice | 45 °C | HS was imposed at reproductive stage for six hours. | HS reduced seed setting rate, grain quality, and reduced chlorophyll contents. | [49] |
| Wheat | 28 °C | HS was imposed at grain filling stage of crop. | HS reduced grain size, grain width, grain moisture, and protein and phenolic contents. | [50] |
| Maize | 45 °C | HS was imposed at seedling stage for twenty minutes. | HS decreased the photosynthetic activity, chlorophyll fluorescence, and electron transport, and induced oxidative stress. | [51] |
| Soybean | 36 °C | HS was imposed for twenty seven days. | HS reduced seed oil concentration, protein concentration, $CO_2$ assimilation, stomatal conductance, efficiency of PS-II, and seed protein contents. | [52] |
| Brassica | 32/22°C DNT | HS was imposed for seven days at first open flower stage. | HS decreased the number of branches, pod number, and seed yield, chlorophyll contents, stomata conductance, pollen viability, and harvest index. | [53] |
| Barley | 35 °C | HS was observed at anthesis stage. | HS reduced grains size, grain number and pod number, chlorophyll contents, RWC, and grain weight. | [54] |
| Groundnut | 32 °C | - | HS decreased photosynthetic activity, damage to thylakoid membrane, and reduced seed setting rate and seed weight. | [55] |
| Tomato | 38 °C | Plants were exposed to HS for four days at seedling stage. | HS significantly reduced the stomatal conductance, chlorophyll contents, transpiration rate, photosynthetic rate, carotenoid content, and biomass. | [56] |
| Lentil | 33 °C | HS was imposed after 50% flowering. | HS damaged cell membranes and reduced chlorophyll contents, chlorophyll fluorescence, photosynthetic rate, and grain protein contents. | [57] |

DNT: day and night temperature.

HS also affects the plant osmotic adjustments (Figure 1) by increasing the evapotranspiration, which affects the solute production in plants that plays an important role in osmotic adjustments [2]. HS also decreases the rate of photosynthesis, while it increases respiration and photo-respiration, which in turn reduces assimilates production and causes a reduction in growth and biomass production [58]. Moreover, HS also disturbs cell metabolism, due to hampering the water balance created as a result of a reduction in water uptake by roots and an increase in water loss from plant leaves [59]. HS also reduces the cell water potential and induces the production of ROS that damage the cellular membrane and increase electrolyte leakage, and, therefore, cause significant yield losses [60,61].

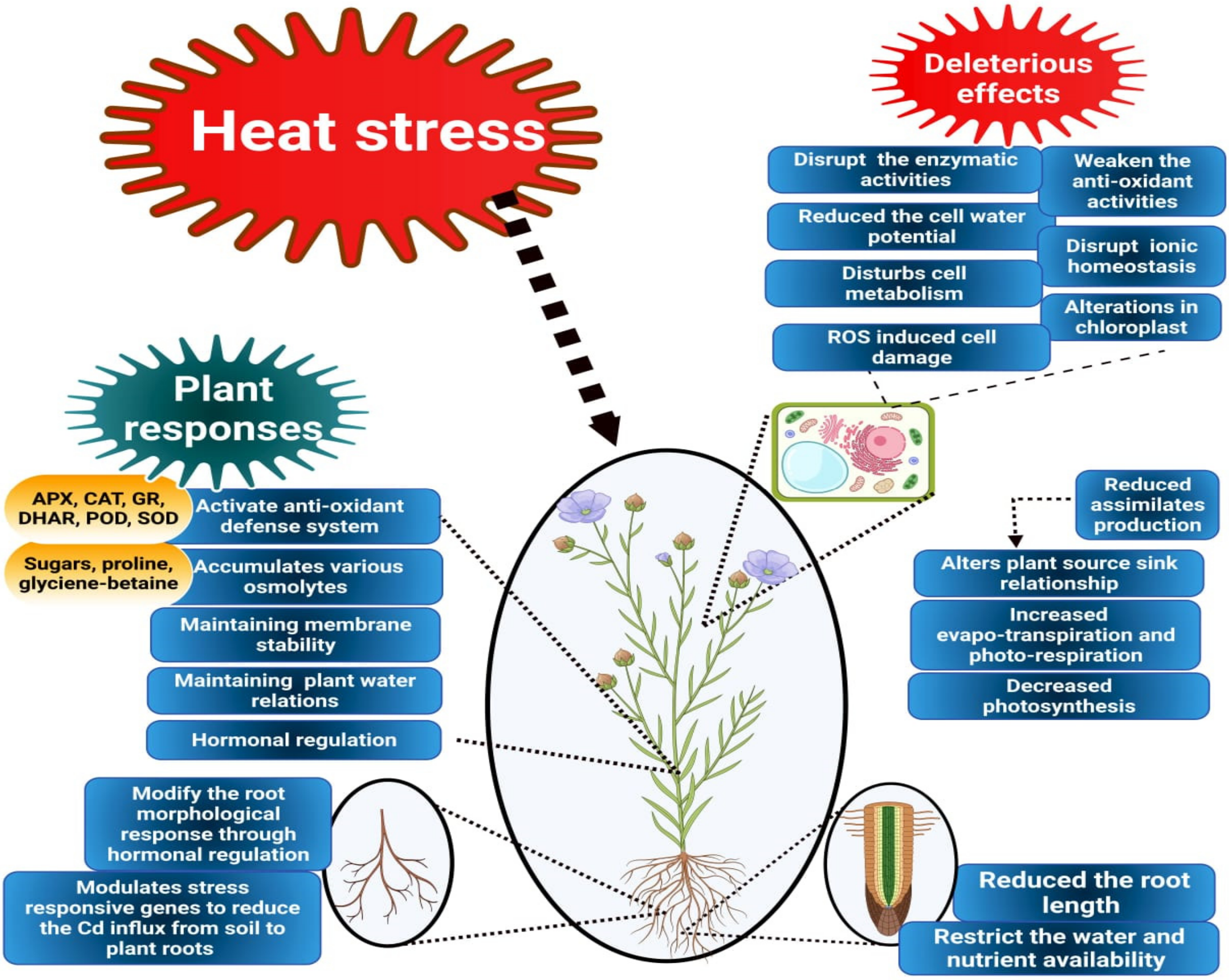


**Figure 1.** Effect of HS stress on plants. HS disturbs cell membranes, plant physiological functioning, photosynthetic efficiency, reduces assimilate production, alters source–sink relationships, root growth, nutrient and water uptake, and results in reduction in growth and yield. Moreover, HS, also dustups enzymatic activities, ionic homeostasis, antioxidant activities, and induces production of ROS, which causes huge growth and yield losses.

Heat stress also decreases the uptake of both nutrients and water, which is a major reason for heat induced reductions in growth and yield [62]. Heat stress also alters the plant source–sink relationship and nutrient accumulation in plants [63]; however, this reduction in nutrient uptake depends on the plant species and soil nutrient status and stress conditions. HS also disturbs the enzymes involved in nutrient metabolism; therefore, decreasing the uptake and accumulation in plants [64,65]. Moreover, HS also reduces the nutrient acquisition, owing to a reduction in root growth, root biomass, and nutrient uptake by roots [2]. Additionally, HS also depletes labile carbon and restricts the translocation of carbohydrates from shoot to root; and the functioning of proteins and causes a significant decrease in nutrient uptake [63].

Photosynthesis is one of the most important processes in plants that are considered to be very sensitive to HS [66]. HS strongly affects the photosynthetic efficiency in both $C_3$ and $C_4$ plants [67]. Heat injury affects the carbon metabolism and thylakoid reactions and causes alterations in chloroplasts and disorganizes the thylakoid; therefore, all these changes result in a significant reduction in photosynthesis under HS [48,68]. HS also reduces the activities of PS-II, Fv/Fm ratio, synthesis of photosynthetic pigments, stomata conductance, leaf water contents, and intercellular $CO_2$ concentration, which also contributes to a reduction in photosynthesis [69–71]. High temperature also reduces the activities of source and sinks and causes a significant reduction in growth and biomass production [2].

HS affects the plant source and sink relationships by reducing the carbon assimilation and partitioning and distribution of C and N in plants [72]. These alterations negatively affect the leaf protein and starch metabolism, which is considered a cause for the reduction in final production and quality [67]. All stages of plant life are sensitive to HS; however, the reproductive stage is considered the most sensitive stage and an increase of a few degrees in temperature at this stage can cause significant yield losses [73]. HS at the reproductive stage reduces floral buds and causes abortion of flowers, which depends on plant species and the severity of stress [74]. Moreover, HS at the reproductive stage also reduces the fruit setting and decreases the grains retained by stigma, which causes seed sterility and consequently reduced final production [75].

Respiration is significantly increased with increasing temperature up to 50 °C; however, after 50 °C, respiration is significantly decreased, due to heat induced damage to respiratory mechanisms [76]. HS also reduces ATP production and causes a significant increase in ROS that damage cellular membranes, protein, lipids, and DNA, and denatures enzymatic activities [77]. However, plants activate an antioxidant defense system comprising different antioxidant enzymes (APX, CAT, GR, DHAR, POD, SOD) to cope with the heat-induced ROS production [2]. Plants also accumulate various osmolytes, such as sugars, proline, glyciene-betaine, and different hormones to counter the effects of HS [74]. The accumulation of these osmolytes improves plant survival by protecting the cellular membrane, antioxidant activities, and maintaining membrane stability and plant water relations [2]. Plant hormones play a crucial role in plant responses to different stress conditions. HS clearly influences the synthesis, degradation, and allocation of hormones to different plant organs, which indicates that they also play a significant role in plant responses to HS [2].

## 3. Melatonin Biosynthesis in Plants

Tryptophan (TP) is a precursor of MT, and the entire process starting from TP to MT is completed by four different enzymes (Figure 1). The first enzyme, named tryptophan decarboxylase (TDC), converts the TP into tryptamine, and after that, another enzyme (tryptamine 5-hydroxylase T5H) converts tryptamine into serotonin (ST) [78], which is considered the main pathway of ST biosynthesis in plants. However, another biosynthesis pathway of ST is present in plants such as St. John's wort (*Hypericum perforatum*) and it is the same pathway that involves MT biosynthesis in animals [79]. ST is converted into N-acetyl-serotonin (NAS) by reaction of *N*-acetyltransferase (SNAT) or arylalkylamine N-acetyltransferase (AANAT). After that, NAS is converted into MT with the help of N-acetylserotonin methyltransferase (ASMT) or hydroxyindole-*O*-methyltransferase (HIOMT). Moreover, SNAT also converts tryptamine into N-acetyl-tryptamine; however, T5H cannot convert *N*-acetyl-tryptamine into *N*-acetyl-serotonin [80]. Additionally, ST can also be converted into 5-methoxytryptamine (5MT) with the help of HIOMT and, finally, 5MT is converted into MT by SNAT [81]. Recently, a reverse pathway of MT biosynthesis has been discovered, in which NAS deacetylase catalyzes N-acetyl-serotonin into ST [82]. TP is also a precursor of IAA (indole-3-acetic acid), and the TP pathway is one of the important pathways of IAA synthesis. In this pathway, TP is catalyzed into tryptamine, after that tryptamine is converted into IAA as an intermediate, with the help of indole-3-acetaldehyde as an intermediate [68]. This shows that MT might have similar impacts on plants such as IAA [83].

## 4. Heat Stress-Induced Melatonin Biosynthesis in Plants

MT is an important signaling molecule and it plays a significant role in plants under different stresses. The synthesis of MT occurs in plant chloroplasts and mitochondria [84], and its synthesis has been reported in fruit trees, crops, and herbs [85,86]. The level of MT in plants is influenced by seasonal, as well as circadian, rhythms [87]; however, the endogenous MT concentration varies significantly in diverse plant species, plant organs, stress conditions, and stages of plant development [88,89]. For instance, MT concentration is significantly increased in tomato and morning glory plants during maturity stages [90]. Light conditions also significantly affect the endogenous MT, and tomato and rice plants grown under field conditions accumulated more endogenous MT compared to plants grown in growth chambers [86,91].

MT is an important antioxidant, and it interacts with ROS and reduces their concentration under stress conditions ([85]. This indicates that the increase in endogenous MT under stress is linked with an increase in ROS production [85]. The concentration of MT in grapevine, barley, and lupin was significantly increased after the imposition of salt and osmotic stress [88]. Similarly, in rice plants, endogenous MT also substantially increased upon exposure to HS [92]. *N*-acetylserotonin methyltransferase (ASMT) enzymes effectively increased endogenous MT and protected plants from the damaging impacts of HS by increasing the expression of heat shock protein [93]. In another study, [92] reported that HS increased the synthesis of endogenous MT in plants, which was linked with an increase in the activities of enzymes involved in MT biosynthesis [94]. Furthermore, *Phacelia tanacetifolia* also showed a substantial increase in MT upon exposure to HS, which protected the plants from HS-induced deleterious impacts by stimulating antioxidant activities [95,96]. These findings indicated that stress conditions induced endogenous MT biosynthesis, which indicates its role in plant responses under different stressful conditions [96]. MT accumulation in plants is linked with gene expression and the activities of enzymes involved in MT biosynthesis. The increase in expression of genes and enzymatic activities involved in MT synthesis significantly increased the MT synthesis in plants grown in stress conditions [86,92,97]. The concentration of MT is closely related to the availability of precursor [97]; therefore, increasing precursor availability can increase MT synthesis under stress conditions [98].

## 5. Melatonin a Promising Substance to Improve Plant Performance under HS

HS is serious abiotic stress, and its intensity in recent times has been substantially increased due to global warming and climate change. HS is a serious concern, and it induces leaf senescence; disrupts physiological, biochemical, and metabolic processes; and, therefore, causes a substantial reduction in growth and final production [99]. MT is an important signaling molecule that improves plant functioning and leads to substantial increases in growth and development under stressed conditions [100–102]). Additionally, MT is also a well-known antioxidant and scavenges ROS and protects plants from stress-induced oxidative damage and improves plant performance [100,103,104].

### *5.1. Melatonin Modulates Plant Growth and Development*

HS significantly reduces plant growth and development and causes a substantial reduction in final production (Figure 2). MT is a naturally occurring molecule that substantially improves plant performance under stress conditions [31]. Seed germination is significantly reduced under HS, which in turn reduces the stand established and the desired population. MT application (1000 μM) improved germination by 60% in *Arabidopsis thaliana,* owing to its stronger antioxidant activities under HS compared to the control [105]. MT also improved the root architecture, reduced leaf senescence, and led to a substantial improvement in plant growth under HS [106–108].

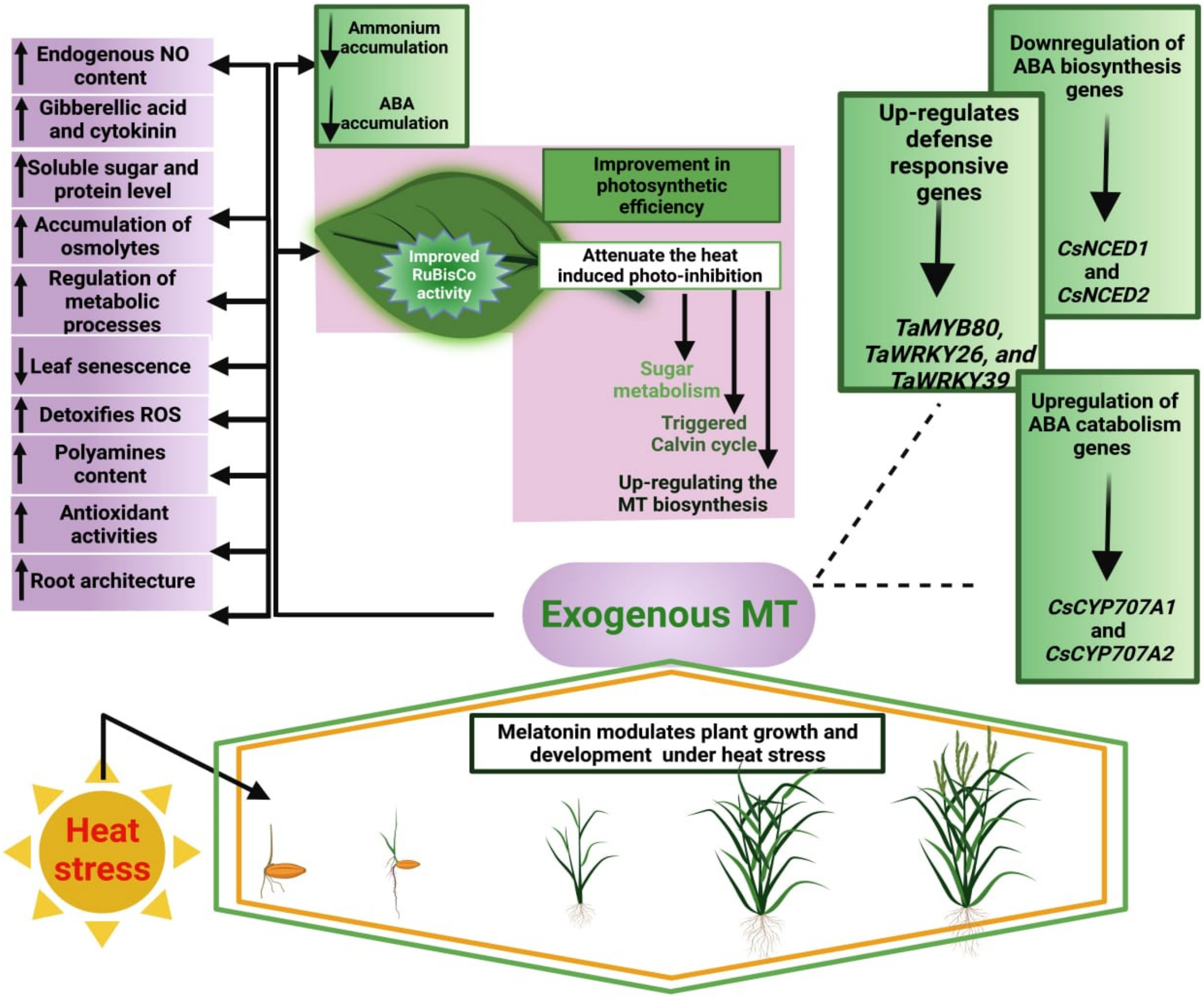


**Figure 2.** MT application protects the photosynthetic apparatus, and improves gene expression, osmolytes accumulation, maintains metabolic processes, improves polyamines and hormones accumulation, and decreases leaf senescence and ROS, resulting in a marked improvement in growth under HS.

MT application appreciably detoxifies ROS and modulates antioxidant activities, which reduces the heat-induced oxidative stress and improves plant growth and development [107]. An exogenous supply of MT also increases the expression of HSPs and delta 1-pyrroline-5-carboxylate synthetase (P5CS) gene, which helps to detoxify ROS and leads to an improvement in plant growth under HS [107]. Moreover, MT also improved the concentration of polyamines (PAs: putrescine, spermidine and spermine) and amino acids, and upregulated the expression of stress responsive genes, which consequently improved the plant tolerance to HS [107,109]. Exogenous supplementation of MT also increased endogenous nitric oxide (NO) contents, activities of nitrate reductase, and upregulated the transcription of MYB and WRKy in tea; therefore, resulting in significant improvements in growth and development [107,110]. In another study, it was noted that an exogenous spray of MT (100 µM) significantly increased the photosynthesis and biomass production by 28.10% and 10.20%, by increasing the expression of MT biosynthesis genes and the accumulation of amino acids [109].

HS stress induced the production of ROS, which cause damage to the photosynthetic apparatus and cause a reduction in the overall photosynthetic efficiency of plants. The exogenous application of MT (50 mM) reduced ROS production, MDA, $H_2O_2$, and electrolyte leakage (EL), and increased the chlorophyll contents (Table 2) and protein contents, by increasing the activities of antioxidant enzymes (CAT, POD, and SOD) and gene expression, resulting in a significant improvement in growth under HS ([111]. In another study, it was reported that MT application (20 µM) significantly improved the root and shoot growth and biomass production, by increasing the chlorophyll synthesis and total soluble proteins (TSP), and decreased the MDA and $H_2O_2$ accumulation, by improving the antioxidant activities (CAT, POD, and SOD) in tall fescue (*Festuca arundinaceous*) [112]. An exogenous supply of MT also maintains the nutrient and water uptake, which in turn improves the photosynthetic efficiency and results in significant improvements in growth and development [113].

**Table 2.** Effect of melatonin on growth and physiological attributes under heat stress.

| Crop | Heat Stress | MT Application | Effects | References |
|---|---|---|---|---|
| Tomato | HS (42 °C) was imposed at seedling stage for seven days. | 100 µM MT was applied 7 days after exposure to HS. | MT application improved the root and shoot growth, biomass production, membrane stability, and chlorophyll contents. | [107] |
| Tomato | HS (38 °C) was imposed 7 days after fourth lead stage. | 100 µM was applied at fourth leaf stage. | MT reduced leaf senescence and leaf yellowing, and enhanced photosynthetic activity and chlorophyll contents. | [99] |
| Cherry Radish | HS (35 °C) was applied at seedling stage. | 67.0 mg $L^{-1}$ was applied 7 days after imposition of stress. | MT foliar spraying significantly enhanced biomass chlorophyll contents, RuBisCo activity. | [114] |
| Wheat | HS (40 °C) was imposed at seedling stage. | 100 µM was applied 15 days after sowing. | MT improved growth rate, leaf area, stomata conductance, photosynthetic and transpiration rates, the photosynthesis rate, and chlorophyll contents. | [5] |
| Ryegrass | HS (38 °C) was imposed after 30 days of sowing. | 20 µM was applied two days before imposition of HS. | MT foliar spraying increased chlorophyll contents, plant height, dry weight, chlorophyll contents, photosynthetic rate, membrane stability, endogenous cytokinins, and reduced the ABA accumulation. | [115] |
| Tall fescue | HS (42 °C) was imposed at seedling stage. | 20 µM was applied before imposition of HS. | MT supplementation increased shoot fresh weight, root fresh weight, chlorophyll, and carotenoid contents | [112] |

### *5.2. Melatonin Maintains Membrane Stability and Plant Water Relationships*

HS significantly disturbs the conformation of membrane proteins, which affects the integrity and functioning of the membrane system. The dysfunction of membranes in response to HS is determined by measuring the EL from the cell membrane [116]. An increase in EL indicates that membrane integrity has been significantly lost owing to the damaging effects of HS [21,60]. However, MT appreciably maintains the membrane integrity and reduces the EL upon exposure to HS. The application of MT substantially increased the antioxidant activities and significantly reduced the EL and MDA accumulation by maintaining membrane integrity [117]. In another study, it was noted that MT application (10 µM) significantly reduced MDA and $H_2O_2$ accumulation by 68% and 49%, and appreciably increased the membrane stability under HS [118]. The upregulation of transcripts and antioxidant activity (APX and SOD) reduced the lipid per-oxidation; however, MT deficiency can cause a significant increase in lipid peroxidation under HS [103,119].

Plants exposed to HS showed a sharp increase in MDA, which damaged the membrane and caused an increase in EL; however, MT decreased MDA and EL (Table 3) by repairing the disrupted membrane and reducing the heat-induced oxidative damages by balancing ROS in high-temperature conditions [107,120]. The foliar supplementation of MT (10 µM) reduced the heat-induced photo-inhibition, by increasing the expression of ASMT gene, which in turn reduced the EL and efficiency of PS-II, by increasing antioxidant activities [93]. Heat-induced water deficiency disturbs plant water relations and inhibits the growth and photosynthetic efficiency of plants. MT application alleviates heat-induced oxidative damage and improves the water uptake and reduces the water loss, thereby maintaining higher RCW under HS and subsequently improving the thermo-tolerance of plants [121].

**Table 3.** Effect of melatonin application on various oxidative stress markers under heat stress.

| Crop | Heat Stress | MT Application | Effects | References |
|---|---|---|---|---|
| Wheat | HS (42 °C) was applied at seedling stage. | 100 µM was applied for 7 days before application of HS. | Melatonin supply improved membrane permeability, and reduced the MDA and $H_2O_2$ accumulation. | [32] |
| Tall fescue | HS (42 °C) was imposed at seedling stage | 50 mM was applied before imposition of HS. | Exogenous MT application reduced ROS level, MDA content, and electrolyte leakage. | [111] |
| Tomato | HS (42 °C) was imposed at fourth leaf stage. | 20 µM was applied 7 days after HS. | MT reduced ROS accumulation and MDA accumulation. | [119] |
| Soybean | HS (42 °C) was imposed at trifoliate leaf stage. | 100 µM was applied five days before imposition of HS. | MT reduced $H_2O_2$ production, lipid per-oxidation, MDA accumulation, and electrolyte leakage. | [122] |
| Chrysanthemum | HS (40 °C) was imposed at seedling stage. | 200 µM was applied for 6 days before HS. | MT reduced MDA and $H_2O_2$ production and rate of superoxide anion production. | [123] |
| Creeping bentgrass | HS (35 °C) was applied to 30-day-old seedlings. | 200 µM was applied two weeks before stress imposition | MT significantly increased membrane stability and reduced the EL. | [117] |

### *5.3. Melatonin Improves Water Use Efficiency and Nutrient Uptake*

The closing of stomata is considered the first line of defense against heat and drought stress. Plant water use efficiency (WUE) is significantly decreased under HS, owing to a reduction in stomata conductance. Any change in stomata movement affects the photosynthetic efficiency of plants, owing to denaturation of the proteins linked with the photosystem [2]. MT application substantially improved the stomata conductance and reduced the canopy temperature, which increased the water loss; therefore, maintaining better WUE and photosynthetic efficiency under HS conditions [124]. HS also reduced the transpiration, owing to a reduction in stomata movements; however, MT application increased the rate of transpiration against heat-induced stomata closure; therefore, maintaining a higher WUE in plants facing HS [103,113].

Nutrient absorption is necessary for plants because they play a significant role in plant physiological, biochemical, and metabolic functioning. HS conditions diminish the water influx through the roots, owing to a decrease in membrane fluidity that reduces the turgor pressure of cells [125]. MT application improves the vapor pressure deficit between the atmosphere and leaf surface, enabling the plant roots to take up more water and nutrients under stress conditions [5]. The application of MT maintains the root activity and improve water uptake, which in turn increases the uptake of N, P, Ca, K, and Mg and improves the plant performance and plant tolerance against HS [126]. In another study, it was reported that the application of MT appreciable increased Ca under HS. The increase in Ca uptake protected the cellular membranes and reduced the heat-induced MDA and $H_2O_2$ accumulation in plants growing under HS conditions [127]. These authors also noted that the application of MT appreciably improved the uptake of other nutrients, including K, Mg, P, and N, resulting in a substantial improvement in growth performance and tolerance against HS [127].

### *5.4. Melatonin Protects Photosynthetic Apparatus and Improves Photosynthesis*

Photosynthesis is one of the most important plant processes that is negatively affected by HS [2]. HS causes chlorophyll degradation and significantly disturbs chlorophyll synthesis; however, MT application substantially detoxifies ROS and maintains optimum chlorophyll synthesis and protects the chlorophyll from degradation under HS [128]. HS reduced the concentration of chlorophyll and carotenoids content in tall fescue, but MT foliar spray significantly improved the concentration of both chlorophyll and carotenoids contents; evidenced by greener leaves in MT treated plants [112]. MT supplementation also facilitates photosynthetic carbon assimilation in tomato plants by triggering the Calvin cycle enzyme gene (sedoheptulose-1,7-bisphosphatase), resulting in significant improvements in the photosynthetic efficiency of plants [33,77]. High temperature decreased the chlorophyll and carotenoid contents; however, exogenous supply of MT appreciably restored the aforementioned photosynthetic pigments under HS compared to the control [100]. Moreover, MT supplementation also significantly increased chlorophyll fluorescence, electron transport rate, the efficiency of PS-II, and photochemical quenching coefficient, resulting in a significant increase in photosynthetic efficiency and plant growth [100].

An exogenous supply of MT can attenuate the heat-induced photo-inhibition by increasing the sugar metabolism and upregulating MT biosynthesis [100]. The application of MT increased the endogenous MT concentration and expression of MT biosynthesis genes that might have increased the chlorophyll contents under HS [92,99]. RuBisCo is considered to be a rate-limiting enzyme for RuBP carboxylation, and it is the primary hub of any stress conditions. HS significantly reduced the RuBisCo activities and expression of genes (rbsL and rbcS) linked with RuBisCo activity. MT application significantly improved the expression of these genes and maintained higher photosynthetic efficiency under HS [99]. HS significantly reduced the FBPase activity and led to a significant reduction in plant photosynthetic performance under HS. MT supply improved fructose-1,6-bisphosphatase (FBPase) activity and gene expression of its encoding enzyme, which in turn improved the plant photosynthetic efficiency in plants growing under HS [99]. Chlorophyll fluorescence is considered an important tool to research plant photosynthetic properties under different stress conditions [129]. Melatonin application reduced the adverse effects of HS, by increasing qP and decreasing the nonphotochemical chlorophyll fluorescence quenching (NPQ) under HS, which indicates that MT reversed the heat induced damage to the photosynthetic machinery [99]. An optimum photosynthetic electron transportation ensures the optimum energy flow, which maintains plant growth and development under normal and stress conditions [130]. An exogenous supply of MT maintains electron transportation and sustains the plant's photosynthetic activities, resulting in significant improvements in plant growth under HS [99,103].

### *5.5. Melatonin Maintains Osmolyte and Hormone Crosstalk*

The osmolytes play an important role in protecting plants from the damaging effects of HS [2]. These osmolytes improve the physiological processes and plant acclimatization under stress conditions. The application of MT increased the endogenous MT contents, which contributed to a significant increase in the expression of photosynthesis genes and the activity of PS-II [100]. MT application to *Lolium perenne* increased the endogenous MT and cytokinin contents, while it reduced ABA accumulation and protected the proteins from oxidizing and misfolding under HS [93,115]. The exogenous supplementation of MT increased the biosynthesis of an enzyme related to nitrogen metabolism and nitrate contents, and reduced the ammonium accumulation and provided protection to cucumber seedlings grown under HS [131]. In another study, it was noted that MT application significantly increased the accumulation of total soluble proteins and led to significant improvements in the growth of tall fescue under HS [112].

Exogenous supplementation of MT significantly increased the endogenous gibberellic acid (GA) and decreased ABA accumulation in plants exposed to HS. The application of MT repressed the transcript abundance of ABA biosynthesis and signaling genes; however, it regulated the expression of MT and GA biosynthesis, which, therefore, led to an increase in GA and MT, while there was a reduction in ABA accumulation [100]. An increased MT and GA accumulation controlled the heat-induced senescence in plants [100]. ABA and salicylic acid (SA) are important hormones that play a significant role in plant response under stress conditions. ABA production in plant cells is linked with ROS formation, and ABA accumulation leads to a significant increase in $H_2O_2$ accumulation [132]. Exogenous MT has been shown to decrease ABA content and downregulate its biosynthesis gene (NCED), while upregulating its catabolic genes, including CYP707A1 and CYP707A2 [115,133]. Many other authors also noted that MT application decreased the ABA accumulation and increased the cytokinin biosynthesis content in plants grown under HS [115,134]. Plants exposed to HS showed a significant increase in SA; however, SA started declining as stress conditions were prolonged. MT application increased SA concentration by increasing the expression of SA biosynthesis gene (PAL2) during HS and led to a significant increase in plant tolerance against HS [122]. The exogenous supply of MT increased IAA and GA contents, while MT application reduced the ABA accumulation [135]. MT also significantly increased the accumulation of methyl jasmonate (MeJA), which resulted in a significant reduction in $H_2O_2$ [136]. Nitric oxide (NO) is considered to play an important role in cellular homeostasis [137], and MT application increases NO accumulation, which in turn reduces the oxidative damage by increasing antioxidant activities [138]. Moreover, IAA also has a positive association with MT, and it has been reported that IAA application increased the endogenous MT [139].

In another study, Buttar et al. [32] noted that MT application increased the endogenous MT contents and expression of stress responsive genes (TaMYB80, TaWRKY26, and TaWRKY39) under HS stress [32]. Similarly, other authors also noted that exogenous MT induced heat tolerance by increasing endogenous MT concentrations [93,94]. The application of MT increases the expression of MT synthesis enzymes (*N*-acetylserotonin methyltransferase); therefore, this leads to a significant increase in endogenous MT under HS [93]. The application of MT also promotes the accumulation of osmolytes, to confer heat tolerance to plants. For instance, it has been reported that MT treatment enhanced the proline (Pro), trehalose (Tre), and total soluble sugars (TSS) accumulation in the roots and sprouts of maize and promoted HS tolerance in maize plants [140]. In another study, Manafi, et al. [141] reported that heat stress increased the Pro contents in strawberry plants, which were further increased by MT (50 μM). The increase in Pro accumulation increased the thermo-tolerance by increasing antioxidant activities [141].

### *5.6. Melatonin Regulates Accumulation of Secondary Metabolites*

Secondary metabolites play a critical role in the signaling transduction of plants, which is considered beneficial for counteracting the effects of different stresses [142]. Previously, different authors noted that MT has a positive-regulator impact on the development of plants and abiotic stresses, by interacting with the polyamines (Pas) signaling pathways [143,144]. MT mitigates the heat-induced oxidative damages by interacting with the PA and NO biosynthesis pathways. Exogenous supply of MT upregulates PAs biosynthesis genes (ADC1/2, SAMDC1/2, SPMS, and SPDS1/2/3/5/6), which favors a better synthesis of PAs under HS [107]. In another study, Alam et al. [111] stated that long-term HS plants treated with MT showed a significant improvement in their heat tolerance, through modulation of PA metabolism. MT along with NO has the potential to combat different stresses through the L-arginine and PAs metabolic pathways. However, the nitric oxide synthases (NOS) and nitrate reductase (NR) pathways are also regulated by PAs [145].

The application of MT upregulates the NO contents, the activities of NOS and NR, and expression of their genes, which indicates that MT promotes NO activity under HS [107]. The phenolic and flavonoid compounds possess excellent antioxidant and ROS scavenging activities under stressful conditions. The application of MT significantly increased the total phenolic (TFC), total flavonoid (TFC), and antioxidant (DPPH) activity, by 90.50%, 73.10%, and 54.30%, respectively, under HS compared to controls [122], which increased the HS stress in plants. An exogenous supply of MT significantly increased the level of free PAs (putrescine; Put, spermidine; Spd, spermine; Spm) in plants and enhanced the HS tolerance, by increasing antioxidant activities [107].

### *5.7. Melatonin Strengthens the ROS and Antioxidant Defense System and Detoxifies ROS*

Heat-induced oxidative stress is one of the major damages to plants, and causes damage to plant proteins, DNA, and lipids [11,146–149]. However, plants activate an excellent antioxidant defense system to cope with the damage of heat induce oxidative stress [2]. Generally, CAT and GPX enzymes scavenge $H_2O_2$ at diverse cellular compartments and are considered to be a major regulator of $H_2O_2$ homeostasis in plant cells. MT is considered a dynamic antioxidant that widely stimulates cellular redox homeostasis by increasing the activities of antioxidant under HS [104,150]. An exogenous supply of MT (70 μM) significantly increased the activities of CAT, GR, and GPX, which in turn reduced the heat-induce damaging effects in maize seedlings [140]. Similarly, other authors also noted that MT directly scavenges ROS, by activating the antioxidant defense system [151,152]. MT works as a signaling molecule and reinforces the activities of antioxidants in plants and, therefore, improves the HS tolerance [140]. MT supplementation also maintained higher activities of AsA, GSH, CAT, GPX, GR, and SOD and ratios of the AsA/(AsA + DHA) and GSH/(GSH + GSSG), reduced the production of ROS, and improved the thermo-tolerance [153].

In another study, Jahan et al. [107] noted that exogenous MT improved the activities of APX, CAT, GPX, and SOD compared to the control and resulted in a significant improvement in thermo-tolerance [107]. According to Wang et al. [154], exogenous MT application increased endogenous MT and expression of MT biosynthesis genes and decreased the ROS accumulation, by increasing the activities of APX, CAT, GPX, and SOD under HS stress. MT foliar spraying improved the activities of AsA and GSH in plants, which suggested that MT application improved the antioxidant activities under HS [155,156].

The AsA-GSH cycle represents an important way to eliminate the production of free radicals in plants. MT application increased the production of AsA and GSH, which led to lower production of $H_2O_2$ under heat and drought stress [157,158]. Buttar et al. [32] also found that MT application improved the APX and GR (Table 4) activities and improved GSH biosynthesis, which detoxified the ROS and reduced the MDA accumulation in wheat plants grown under HS. Moreover, MT application also lowers the TBARS and $H_2O_2$ content, which was linked with augmented antioxidant activities. The increase in antioxidant activities also increased the photosynthetic and carbohydrate metabolism to provide energy and a carbon skeleton to plants growing under HS [5]. Additionally, MT treatments also activated APX, CAT, GSH, Gly-I, Gly-II, GR, and SOD, by increasing their genes expression (Table 4), and subsequently improved the thermo-tolerance in plants [140]. The increase in the activities of antioxidant enzymes laid the foundation for the acquisition of HS tolerance in plants. The activation of antioxidant defense system is one of the most important physiological mechanisms of MT-induced HS tolerance in plants. Therefore, it is suggested that there is a dynamic relationship between the MT and antioxidant signaling pathways, which helps to develop HS tolerance in plants.

**Table 4.** Effect of melatonin on the accumulation of various osmolytes, antioxidant activities, and gene expressions under heat stress.

| Crop | Heat Stress | MT Application | Effects | References |
|---|---|---|---|---|
| Strawberry | HS (40 °C) was applied at seedling stage. | 100 µM was applied two days before imposition of HS. | MT supplementation improved the proline accumulation and increased the activities of APX, CAT, GPX, and GSH, and expression of heat shock proteins. | [141] |
| Wheat | HS (42 °C) was imposed at seedling stage. | 100 µM was applied 7 days before HS. | MT application increased the activity of antioxidant enzymes, including SOD, CAT, and POD. | [32] |
| Tomato | HS (40 °C) was applied to 8 week old seedling. | 10 µM was applied 8 h before HS. | MT spray enhanced HSP expression to refold denatured and unfolded proteins under heat stress. | [93] |
| Kiwifruit | HS (45 °C) was imposed at seedling stage. | 200 µM was applied before HS. | MT application enhanced the carotenoid biosynthesis and regulated the expression of HSPs, to mitigate HS effects. | [159] |
| *Pinellia ternata* | HS (35 °C) was applied at seedling stage. | 100 µM was applied 7 days after HS imposition. | Exogenous application of MT increased expression of HSPs, to confer heat tolerance. | [134] |
| Tomato | HS (40 °C) was applied at seedling stage. | 50 µM was applied 7 days after HS imposition. | MT application increased the GR, MDHAR, DHAR, GST, SOD, POD, and CAT activities and increased the accumulation of NO and polyamines. | [160] |
| Peppermint | HS (40 °C) was imposed at seedling stage. | 30 mM was applied after 40 days of sowing. | MT alleviated adverse effects of HS by increasing the activity of CAT, SOD, GST, and POX. | [121] |

### *5.8. Melatonin Up-Regulates the Defensive Genes*

MT application appreciably improved the expression of stress responsive genes (FaTHsfA2a, HSP90, and FaHsfB1a), to confer heat tolerance in plants [94]. For instance in *Arabidopsis*, MT application significantly increased the expression of A1 heat-shock factors (HSFA1s) [94]. Moreover, exogenous supply of MT also triggered the thermal responsive genes transcripts (HSFA2, HSP90, and HSP101), which participate in inducing HS tolerance [94]. Heat shock protein (HSPs) has a close association with HS, and over-expression of HSP-70 substantially improved the HS tolerance [161]. An exogenous supply of MT significantly increased the expression of different HSPs (HSFB3, HSFA1a, HSFA2b, HSP23, HSP70, HSP80, and HSP90), which in turn improved the thermo-tolerance in chrysanthemum leaves [123]). HsfA2 and HSP90 are considered to be key regulators of ROS detoxification through the $H_2O_2$-mediated signaling pathway. The application of MT upregulated the activation of both HsfA2 and HSP90 and conferred HS tolerance in tomato seedlings [107].

A recent study also reported that HsfA2 plays an important role in $H_2O_2$ signaling and improves HS memory subsistence, while HSP90 coordinates in DNA-binding enhancement process and the whole of this process is linked with MT-induced HS tolerance [162,163]. In tomato seedlings, exogenous supply of MT increased the MT biosynthesis and expression of HSP following a substantial increase in thermo-tolerance [93]. Similarly, strawberry plants treated with MT showed an increase in the expression of FaTHsfA2a, HSP90, and FaHsfB1a, which contributed significantly to improvements in HS [141]. The MYB and WRKY transcription factors play an important role regulating complex and dynamic characteristics under HS. An exogenous supply of MT improved the expression of stress responsive genes (TaWRKY39 and TaWRKY26) and substantially increased the thermo-tolerance in wheat plants [32]. Similarly, Du et al. [164] also noted that exogenous MT increased the expression of TaMYB80 gene expression after six hours of HS and led to a significant increase in HS tolerance [164,165]. Additionally, MT also increased the endogenous MT and expression of heat shock factor (HSP), which improved the accumulation of HSPs following a substantial increase in HS tolerance [40,93].

## 6. Success Stories of Engineering Melatonin to Improve Heat Tolerance

The accumulation of various hormones and osmolytes improve the plant's growth and development under different stress conditions. Owing to the promising characteristics of MT, efforts are underway across the globe to develop transgenic plants with enhanced MT levels to confer HS tolerance. Both exogenous MT application, and endogenous MT manipulation, reduce the ROS and maintain better plant growth and development under stress conditions. For instance, a tomato line with over-expression of SlSNAT gene protected the ribulose bisphosphate carboxylase and oxygenase proteins and improved the growth, efficiency of PS-II, Fv/Fm and reduced the heat-induced injury [154]. In cotton, the over-expression of GhM2H gene substantially improved the HS tolerance, by increasing the antioxidant activities, endogenous MT, and reducing the ABA accumulation [166,167]. Moreover, the development of transgenic watermelon melatonin plants with ClCOMT1 genes produced a significant increase in endogenous MT contents, following a substantial improvement in growth and tolerance against cold and heat stresses [168,169]. Moreover, the development of apple plants with ASMT gene showed a significant increase in HS tolerance. The apple plants, upon exposure to cold, drought, and heat stresses, showed a significant increase in expression of ASMT genes, which increased the endogenous MT biosynthesis and improved the tolerance against cold, drought, and heat, by increasing antioxidant activities [170,171]. Ahammed et al. [103] developed MT-deficient tomato plants by silencing the MT biosynthetic genes (COMT1; Caffeic Acid O-Methyltransferase-1). These authors noted that COMT1 silencing increased the HS by inhibiting the light relations and carbon fixation, as well as the efficiency of PS-II reactions and electron transport. Nonetheless, MT application alleviated the heat induced photosynthesis inhibition, which indicates that MT is essential for maintaining plant photosynthetic efficiency under stress conditions [103]. Additionally, in mustard sprouts, an increase in the expression of MT synthesis genes (BjTDC-1, BjTDC-2) and serotonin N-acetyltransferase genes (BjSNAT-1) significantly increased the endogenous MT contents and HS tolerance, by increasing antioxidant activities [172,173].

## 7. Conclusions and Future Prospects

Heat stress induces serious alterations in plant growth and development by disturbing a wide range of physiological, biochemical, and molecular processes and antioxidant activities. However, MT application improves plant performance under HS, starting from seed germination to senescence and providing adaptive immunity against HS. In light of the aforementioned findings, it is concluded that MT application improves the membrane stability, water use efficiency, nutrient homeostasis, and synthesis of photosynthetic pigments, and protects the photosynthetic system from heat induced oxidative damages; thereby, improving plant growth under HS. MT application also improves the accumulation of secondary metabolites, osmolytes, and hormones, and improves antioxidant activities, which protect plants from heat-induced oxidative damages, and plant performance under HS. Besides this, MT also improves the expression of heat shock proteins and stress responsive proteins, which also improves heat tolerance in plants. Additionally, increased endogenous MT also enhances HS tolerance by different pathways, including improved antioxidant activities, osmolyte accumulation, photosynthetic performance, and gene expression by reducing ABA accumulation.

Despite recent progress, there are still many unanswered questions regarding the MT signaling network and the resulting actions in different plant processes. The role of MT in seed germination is poorly studied; therefore, future studies should be aimed at to determine the role of MT in the different processes and mechanisms of seed germination. MT is considered to be an unstable molecule; therefore, its transportation and accumulation to different organs must be explored under HS conditions. The role of MT in nutrient uptake is poorly studied and only limited information is available in the literature on this aspect. Thus, more studies are needed to explore the role of MT in nutrient uptake and nutrient signaling under HS. Moreover, it would also be interesting to explore the role of MT in ionic transporters and nutrients channels under HS. The role of MT in photosynthesis under HS has been well explored; however, its role in stomata signaling is still unknown. Therefore, it would be fascinating to explore the role of MT in stomata signaling and its effects on the regulation of anion channels in guard cells under HS.

The role of MT in pollen viability, grain quality, and reproductive characteristics has not yet been explored; thus, it is mandatory to explore the role of MT in these areas. ROS are mostly produced in chloroplasts and mitochondria, and being a signaling molecule, it would be interesting to explore inter-organelle MT signaling under HS. The role of MT in hormones and osmolytes under HS is also poorly studied; therefore, more studies are needed to explore the role of MT in different osmoregulating compounds and hormones under HS. The complex relationships of MT with salicylic acid, indole acetic acid, gibberellic acid, cytokinin, ethylene, proline, and glycine-betaine must be explored at the transcriptomic level. It would also be fascinating to explore the effect of MT on the genes and enzymes linked with the biosynthesis of the aforementioned compounds under HS. The role of MT is mostly studied under lab conditions, and there is a dire need to conduct long-term studies under different climatic conditions. The effect of MT on defensive genes and interaction with HS has not been well explored; thus, more studies are direly needed on this aspect. Moreover, there is a dire need to elucidate the potential of modern techniques to identify MT-related genes, proteins, and enzymes, to develop heat-tolerant genotypes. The development of advanced omic techniques will allow us to explore MT-mediated HS tolerance in plants at metabolomics, proteome, and transcriptome levels. Finally, engineering MT-mediated metabolic and signaling pathways will surely open a new window into existing knowledge, to explore the MT-mediated HS tolerance mechanisms in plants.

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