





Review

# Melatonin in Plant Defense against Abiotic Stress

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**Abstract:** Abiotic stress adversely affects plant growth and metabolism and as such reduces plant productivity. Recognized as a major contributor in the production of reactive oxygen species (ROS), it hinders the growth of plants through induction of oxidative stress. Biostimulants such as melatonin have a multifunctional role, acting as a defense strategy in minimizing the effects of oxidative stress. Melatonin plays important role in plant processes ranging from seed germination to senescence, besides performing the function of a biostimulant in improving the plant's productivity. In addition to its important role in the signaling cascade, melatonin acts as an antioxidant that helps in scavenging ROS, generated as part of different stresses among plants. The current study was undertaken to elaborate the synthesis and regulation of melatonin in plants, besides emphasizing its function under various abiotic stress namely, salt, temperature, herbicides, heavy metals, and drought. Additionally, a special consideration was put on the crosstalk of melatonin with phytohormones to overcome plant abiotic stress.

**Keywords:** abiotic stress; biostimulants; melatonin; phytohormones; plants



**Citation:** Rehaman, A.; Mishra, A.K.; Ferdose, A.; Per, T.S.; Hanief, M.; Jan, A.T.; Asgher, M. Melatonin in Plant Defense against Abiotic Stress. *Forests* **2021**, *12*, 1404. <https://doi.org/10.3390/f12101404>

Academic Editor:  
Domingo Sancho-Knapik

Received: 8 August 2021  
Accepted: 30 September 2021  
Published: 15 October 2021

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## 1. Introduction

Abiotic stresses including extremes of temperature, drought, salinity etc, greatly influence plant growth and productivity [1–3]. It has been estimated that about 90% of arable land is prone to one of the above-mentioned stresses [4]. Furthermore, abiotic stresses show progressive development under the current era of global climatic change [5,6] and pose a great threat to sustainability in agriculture worldwide. Often correlated with a decrease in the soil water level, any significant reduction in the cultivable capacity of the soil often occurs with a change in the land use pattern from that typical of a fertile to marginal one [7,8]. It affects growth and development of crop plants via a reduction in germination, a decrease in the photosynthetic activity and carbon assimilation to a large extent, decreased flowering, and pollen sterility, and as such, acts as a major limiting factor for crop yield [9–12]. Abiotic stresses affecting different stages of plant growth constitute about 70% of the losses in yield among major crop plants like rice, wheat, corn, etc. [13–16].

Biostimulants include substances of both natural and synthetic origin, that, on applying to plants, influence their growth via changes in vital processes. Biostimulants thereby help in mitigating stress conditions. As stresses often cause frequent remodelling of the plant's defence system as adjustment to the change in environment [17,18], biostimulants prime plants to sensitize and enhance their defence strategies in order to respond effectively in combatting effects exerted by an ever-changing environment [19–23]. Reducing the need of fertilizers, they impart tolerance to different kinds of stresses and as such cause increases

in the crop yield, as well as leading to improvements in the quality of crop product [24,25]. Under continuous exposure to stresses (both biotic and abiotic), the priming of plants by biostimulants offers a novel way to regulate or modify different physiological processes that influence growth and development activities in plants. Stimulation of plant defence machinery is currently being explored as an emerging strategy to enhance crop productivity and resilience to changing climatic conditions. Keeping in view immune priming of plants that offer the potential of imparting resistance against different environmental stresses, the current study was undertaken to elaborate the role of melatonin in plant growth and development, with special emphasis on its crosstalk with plant hormones in enhancing plant productivity, besides having information in promoting and sensitizing plant defense to overcome the ill effects of different abiotic stresses.

## 2. Melatonin as a Bio-Stimulatory Molecule

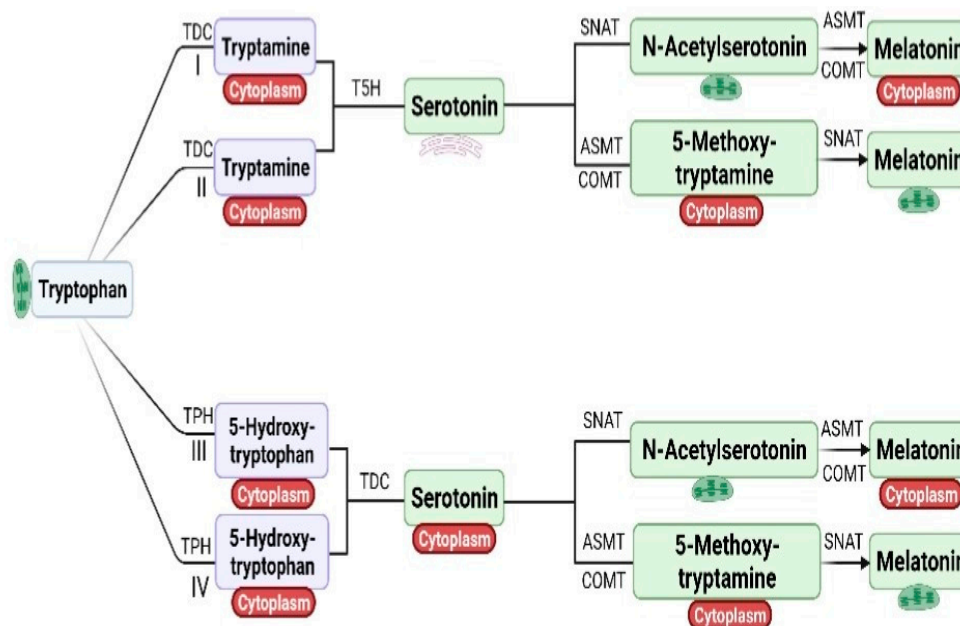
Plant growth regulators are the multifunctional molecules involved in regulating the growth and development of plants, besides attributing the property of abiotic stress tolerance [9,26,27]. Of them, production of melatonin (*N*-acetyl-5-methoxytryptamine) is well established among the majority of monocotyledons and dicotyledons families [28,29]. Despite its production in the mitochondria and chloroplast of roots and leaves, its translocation to meristems, flowers and fruits promotes growth of aerial parts of the plant [30–32]. It is found in higher amounts in reproductive tissues that are young and decline in senescence tissues. In a study, Van Tassel et al. observed that melatonin content is higher in two-day old seedlings of *Pharbitis nil* (L.) compared with older seedlings [33]. In *Brassica juncea* (L.), application of 0.1 mM concentrations of melatonin increases root growth, while higher melatonin concentration (100 mM) was found to exert inhibitory effects on the growth of roots [34]. Melatonin at a concentration of 0.1–0.5  $\mu$ M was found to promote regrowth of the frozen shoots [35]. Enhancement in the germination of *Cucumis sativus* (L.) seeds were observed after treating seeds with 100  $\mu$ M melatonin [36].

## 3. Melatonin Biosynthesis in Plants

Melatonin was first detected in plants in 1995 [37]. Melatonin synthesis in plants was confirmed by an isotope tracer study in *Hypericum perforatum* (L.) [38]. The biosynthesis of melatonin is well established in plants [39–41]. Melatonin, an indolic substance has its origins in serotonin (5-hydroxytryptamine) [29,41,42]. Sharing a common biosynthetic precursor i.e., 5-hydroxytryptophan, their synthesis is reported in both animals and plants [38,41,43]. In one study, the role of the tryptamine pathway (Tryptophan Tryptamine-Serotonin) in the production of serotonin was well established [44]. Melatonin is biosynthesized in four pathways. In plants, tryptophan decarboxylase converts tryptophan into tryptamine in cytoplasm which undergoes further conversion to serotonin upon catalysis by tryptamine-5-hydroxylase in endoplasmic reticulum [29]. The *N*-acetylation of serotonin takes place by enzyme serotonin-*N*-acetyltransferase (SNAT), which converts serotonin into *N*-acetyl serotonin which, upon methylation either by acetyl-serotonin methyl transferase (ASMT) or by caffeic acid *O*-methyltransferase (COMT), respectively, leads to production of melatonin in cytoplasm (Pathway I). Serotonin in presence of either ASMT or COMT is converted into 5-methoxytryptamine in cytoplasm and finally converted into melatonin by SNAT in chloroplast (Pathway II). Tryptophan is converted into 5-hydroxytryptophan by enzyme tryptophan 5-hydroxylase (TPH). 5-hydroxytryptophan is converted into serotonin by Tryptophan decarboxylase (TDC) in cytoplasm. Serotonin in cytoplasm is converted into *N*-acetylserotonin by SNAT and into 5-methoxytryptamine either by ASMT/COMT. *N*-acetylserotonin and 5-methoxytryptamine is converted into melatonin either by ASMT/COMT or by SNAT in cytoplasm and chloroplast respectively [29] (Pathway III and IV).

The biosynthesis of melatonin is briefly described in Figure 1. The Intermediate of Melatonin is found in cytoplasm, endoplasmic reticulum and chloroplasts [29,45]. The expression pattern of genes encoding the biosynthesis of melatonin in salt, drought and

cold stress has been well studied in *Oryza sativa* (L.) [46]. In this study, drought stress was found inducing expression of TDC and ASMT genes, while suppressing the expression of T5H and SNAT. In contrast, salt stress causes up-regulation in the expression of TDC, ASMT, and SNAT genes with suppression of T5H. On the other hand, cold stress (4 °C) causes enhancement in the expression of TDC, while inducing suppression of T5H, SNAT, and ASMT genes. Together, it indicates that stress has a pronounced effect on the expression of different genes of the melatonin pathway.



**Figure 1.** Biosynthesis of melatonin in plants. Abbreviations: TDC, tryptophan decarboxylase; TPH, tryptophan hydroxylase; T5H, tryptophan 5-hydroxylase; SNAT, serotonin *N*-acetyltransferase; ASMT, *N*-acetylserotonin methyltransferase; COMT, Caffeic acid *O*-methyltransferase.

#### 4. Melatonin as Plant Growth Regulator

Melatonin—a signaling molecule that acts as a master plant growth regulator, stimulates plant growth and development, besides providing defense to plants against different stresses [47,48]. As stresses (both biotic and abiotic) affects the growth of the plants and thereby cause a reduction in the yield, production of melatonin in response to these stresses exerts effects similar to indole-3-acetic acid (IAA) in protecting plants via its involvement in multiple physiological processes [15,49,50]. Sharing synthesis from a similar moiety, tryptophan, melatonin performs a regulatory check of plant growth and development [42]. Exogenous application of melatonin causes a reduction in the leaf area in *Arabidopsis thaliana* (L.) [51], increases gas exchange and yield in *Brassica juncea* under salt stress [52], accelerates endogenous levels of melatonin by increasing methyl jasmonate (MeJA) accumulation in *Citrullus lunatus* (Thunb), and increases chlorophyll content in *Zea mays* (L.) on exposure to drought stress [53,54]. It increases germination and photosynthetic activity in *Cucumis* and *Oryza sativa* under cold stress [55,56], increases Fv/Fm ratio for *Solanum lycopersicum* (L.) grown under heat stress [57], and provides tolerance to *Nicotiana tabacum* (L.) against cadmium [58]. Additionally, melatonin was found capable of regulating its own biosynthesis along with the synthesis of prominent plant growth regulators such as auxin, gibberellins, cytokinin's, ethylene, jasmonic acid, and others. Melatonin increases the accumulation of sugars which enhance the endogenous NO level that induces immunity against bacterial pathogens through salicylic acid and NO-dependent pathway. NO triggers melatonin biosynthesis, and on the other hand, melatonin behaves as an NO scavenger. Both these processes induce changes to hormone levels via the up or downregulation of hormone biosynthesis or catabolism enzymes. Melatonin and NO can induce auxin

signaling transduction genes. Melatonin has auxin-like activity as it induces root and shoot growth that gives rise to lateral and adventitious roots. Melatonin's role in fruit ripening and post-harvest processes as a gene of ethylene-related factors is similar [32,45] (Table 1).

**Table 1.** Melatonin functioning in relation to Plant growth regulators under different stress conditions.

Type of Stress	Melatonin Dose	Plant sp.	Plant Growth Regulator	Response	Reference(s)
Cold stress	100 $\mu$ M	<i>Cucumis sativus</i>	NO	Increased Antioxidants provide Cold tolerance. Increased PsbA (D1) protein of PSII. Decreased oxidative stress markers such as electrolyte leakage (EL), MDA, and reactive ROS accumulation.	[59]
	150 $\mu$ M	<i>Citrullus lunatus</i>	JA accumulation	MeJA and H <sub>2</sub> O <sub>2</sub> accumulation increased. Melatonin display role in grafting-induced cold tolerance	[53]
Salinity stress	20 $\mu$ M	<i>Gossypium hirsutum</i> L.	Melatonin regulate ABA and GA genes expression	Increased germination rate, Hypocotyl length, and starch content. Melatonin regulated ABA and GA expression of genes involved in plant signal transduction pathway, and alleviated dormancy	[60]
	10 $\mu$ M	<i>Arabidopsis thaliana</i>	ABA	Melatonin induces salt tolerance through the upregulation of ABA responsive genes, Induce antioxidant defense systems, counteract the salt-induced ROS overproduction	[61]
	70 $\mu$ M	<i>Triticum aestivum</i> (L.)	NO scavengerSA	Increased tissue growth, root and shoot weight, Salinity tolerance Melatonin and SA induce nitrogen metabolism, Melatonin and SA increased the content of Spd, Spm and Pas	[62]
	1 $\mu$ M	<i>Brassica napus</i> (L.)	NO	Decreased lipid peroxidation, hydrogen peroxide content, Redox and ion homeostasis maintenance	[63]
	20 $\mu$ M	<i>Triticum aestivum</i>	H <sub>2</sub> S	Improved photosynthesis, Decreased oxidative stress markers	[64]
High temperature	100 $\mu$ M	<i>Lolium perenne</i> (L.)	ABA, CK	Regulate CK biosynthesis genes, Down-regulation of ABA biosynthesis genes, Melatonin supplementation enhanced the endogenous melatonin and CK content reduced content of ABA under heat stress.	[65]
	100 $\mu$ M	<i>Solanum lycopersicum</i>	PAs, NO	Enhanced PAs levels and regulate transcript abundance, Melatonin increased endogenous NO content, Decreased oxidative stress parameters	[66]

Table 1. Cont.

Type of Stress	Melatonin Dose	Plant sp.	Plant Growth Regulator	Response	Reference(s)
pH stress	5 $\mu$ M	<i>Malus hupehensis</i>	PAs	Enhanced antioxidants PAs content and its gene, Increased MDA	[67]
Drought	20 $\mu$ M	<i>Agrostis stolonifera</i> (L.)	CK	Improved photochemical efficiency, chlorophyll content, up regulates dehydrated genes, Cytokinin-signaling and synthesis genes were prominently up-regulated in ME-treated ipt-transgenic plants.	[68]
Drought + Cold	1 mM	<i>Hordeum vulgare</i> (L.)	Higher ABA accumulation	Better water status, modulating antioxidant systems and ABA levels	[69]
Pb	0.1 mM	<i>Zea mays</i>	NO Scavenger (cPTIO)	MT in combination with cPTIO resulted in an elevation H <sub>2</sub> O <sub>2</sub> , MDA contents, and EL parameters, cPTIO in combination with MT was ineffective in changing the activities of enzyme.	[70]
Cd	100 $\mu$ M	<i>Triticum aestivum</i>	NO scavenger (cPTIO)	Enhanced growth attributes, Decreased oxidative stress, reduced endogenous NO Levels	[71]
Fluoride	20 $\mu$ M	<i>Oryza sativa</i>	Accumulation of gibberellic acid (GA) and endogenous ABA, low indole-3-acetic acid	Decreased oxidative stress, promote root and shoot growth, plant biomass, Decreased oxidative stress, Increased Proline accumulation	[72]

Melatonin's function as a plant growth regulator is owed to its growth-promoting activity and enhancement of yield via the regulation of ion homeostasis [50]. Similarly to auxin and cytokinin, melatonin induces lateral root generation and stimulates root and shoot growth by protecting sub-cellular structures and photosynthetic apparatus and in delaying senescence [45,73]. Melatonin stimulates lateral and adventitious root regeneration and cotyledons expansion in young *Brassica juncea* seedlings and *Lupinus albus* (L.) [34,73]. Its role in regulating the expression of ethylene-related factors adds its role in fruit ripening and post-harvest processes [74–76]. Additionally, melatonin regulates the ABA pathway in *Malus hupehensis* (Pamp) [77] and upregulates key genes in GA biosynthesis [49].

Melatonin helps to overcome the ill effects of stressors and, as such, acts as an important regulator of plant growth [41,78]. Studies have demonstrated the role of melatonin in the detoxification of free radicals (ROS) generated as part of metabolic or photosynthetic activities [39,52,79,80]. High concentrations of melatonin reduce ROS in root cells and thereby inhibit ROS-induced cell growth in *Glycyrrhiza uralensis* (Fisch) [81]. Its effect as an antioxidant helps in controlling the production of reactive oxygen and nitrogen species (ROS, RNS) that impart protection to plants against different stresses [41,42,82]. Melatonin is reported to be more effective than glutathione and vitamin E in the scavenging of ROS and RNS, besides regulating the activity of superoxide dismutase (SOD), peroxidase (POX), catalase (CAT), and glutathione reductase (GSSG-R) [41]. Exogenous application of melatonin activates antioxidant system in plants that has a positive impact in imparting resistance against different environmental stresses via reduction in the oxidation of proteins, lipids, and nucleic acids [50,73,83]. Additionally, melatonin is found to be effective in

increasing the efficiency of mitochondrial electron transport chains and in reducing the leakage of electrons [84,85].

### 5. Melatonin as Stress Reliever

The environmental conditions that favour plant growth greatly influence the melatonin content of the plants. Plants exposed to sunlight have more melatonin than exposed under artificial light [86,87]. The melatonin content shows significant enhancement from 22 (for plants grown in growth chamber) to 142 ng g<sup>-1</sup> f.w (for plants grown in open field) in the leaves of *Solanum lycopersicum* [87]. Interaction between melatonin with other plant growth regulators has been studied under stress conditions (Table 2) and found to alleviate or protect plants from different stresses discussed in detail as below:

**Table 2.** Melatonin functioning under different stress conditions.

Type of Stress	Melatonin Dose	Plant sp.	Response	Reference(s)
Drought	50 µM	<i>Arabidopsis</i>	Regulation of the mRNA expression of various stress-responsive genes such as <i>COR15A</i> , <i>RD22</i> , and <i>KIN1</i> , sucrose accumulation	[88]
	4, 20, and 100 µM	<i>Cynodon dactylon</i> (L).	Reduced reactive oxygen species (ROS), higher antioxidants metabolism, high concentration of amino acids, organic acids, sugars, and sugar alcohols,	[89]
	100 µM	<i>Malus</i>	Better water conservation in leaves, electrolyte leakage less, increased photosynthetic rate. Melatonin down-regulates MdNCED3, an abscisic acid (ABA) synthesis gene and up-regulates catabolic genes MdCYP707A1 and MdCYP707A2. Reduced ABA contents and increases antioxidant enzymes.	[77]
	50 µM melatonin	<i>Zea mays</i>	Plant growth and photosynthetic attributes increases. Antioxidant enzymes activity increases.	[54]
Thermotolerance	20 µM	<i>Arabidopsis</i>	Upregulation of heat-shock factors (HSFA1s)	[90]
	(100 µmol/L)	<i>Zea mays</i> (L).	Increased photosynthesis. Reduced oxidative damage.	[91]
Herbicide Pendimethaline (Pend) ( <i>N</i> -(1-ethylpropyl)-3,4-dimethyl-2,6-dinitrobenzenamine)	8, 16 and 32 mM	<i>Capsicum annuum</i> (L.)	Chlorophyll content and relative water content reduced. Increase in carotenoid, proline and glutathione.	[92]
Paraquat	200 µM	<i>Pisum sativum</i> (L.)	Increased photosynthetic pigments, improved functioning of the photosynthetic apparatus. Increased water content	[93]
Salt	1 µM	<i>Brassica juncea</i>	Increased plant height, leaf length/width, and stem diameter. Increased gas exchange parameters, relative water content. Reduced abscisic acid and increased salicylic acid content.	[52]

Table 2. Cont.

Type of Stress	Melatonin Dose	Plant sp.	Response	Reference(s)
	50, 100, 200, 300, or 500 $\mu$ M	<i>Limonium bicolor</i> (Bunge)	Higher seed germination, high content melatonin, High gibberellic acid (GA), low content abscisic acid (ABA).	[49]
	10 $\mu$ M	<i>Oryza sativa</i>	Decreasing the sodium content to maintain $\text{Na}^+/\text{K}^+$ homeostasis, decreased membrane lipid oxidation, increased chlorophyll content.	[94]
Cold Stress 4 °C	150 $\mu$ M	<i>Citrullus lanatus</i>	Increased accumulation of MeJA and $\text{H}_2\text{O}_2$ , Increased tolerance and Fv/Fm	[53]
4 °C	100 $\mu$ mol	<i>Solanum lycopersicum</i>	Increased Fv/Fm, Increased NPQ	[95]
−5 °C	100 $\mu$ M	<i>Cynodon dactylon</i>	Higher chlorophyll fluorescence transient (OJIP) curves. Arabinose, mannose, glucopyranose, maltose, and turanose) and one organic acid (propanoic acid) increased. Valine and threonine contents reduced.	[96]
Heavy metals (Lead)	200 nM	<i>Nicotiana tabacum</i>	Prevents DNA damage, efficacious antioxidant and decreased superoxide radical accumulation.	[97]

### 5.1. Melatonin under Drought Stress

Drought is the major stress that alters physiological, biochemical, and molecular processes in plants [11,12,98,99]. The plants grown in arid and semi-arid regions will face more intense and longer periods of drought [100]. The urgent need of the hour in these changing environmental conditions is to promote adaptive agricultural strategies because numerous levels of sensitivity to water stress are shown by different organs [12,101]. *Cucumis sativus* exposed to melatonin has a higher rate of germination of seeds and root growth when grown in PEG-stressed conditions [36] and reduced drought-promoted leaf senescence in *Agrostis* [68]. Supply of melatonin in the leaves of *Malus domestica* (Borkh) has been shown to delay the senescence as a result of long-term exposure to drought [102]. Applications of melatonin can more prominently increase whole-plant drought tolerance [77,103]. Water restrictions during growth are responsible for rise of endogenous melatonin, which is four-fold greater than that of well-irrigated plants, indicating the that melatonin has a signaling role in lupin seedlings [87].

Melatonin application at roots causes reduction in the leaf senescence, along with significant improvement in the efficiency of PSII and enhancement in the antioxidative enzymes, that led authors to propose use of melatonin for agricultural purposes [102,104]. A study on mycorrhizal inoculation of tobacco or application of melatonin alone causes enhancement in the nutrient uptake followed by accumulation of osmolytes; thereby leading to increase in the chlorophyll fluorescence, increased seedling growth with reduced drought stress effects [105]. Heshmati et al. reported seed priming in response to melatonin in a dose dependent manner [106]. Melatonin was found enhancing stability of membranous structures with increase in the performance of antioxidant enzymes that confer drought tolerance in *Carthamus tinctorius* L. Additionally, melatonin causes increase in the amount of photosynthetic pigments, osmoprotectants and as such relative water content in *Zea mays* seedlings that progresses with increase in the overall development of the plant and a decline in ROS-mediated oxidative damage [107]. Melatonin contributes to

regulation of C and N metabolism in a coordinated manner; thereby increases its ability of plants to survive under drought stress [108]. Transcriptomic studies of such plants revealed increase in the rate of photosynthesis, N-assimilation, protein biosynthesis under drought stress conditions. The explants of shoot tips of cherry grown in vitro in medium having melatonin showed a 5-fold increase in proline level and 3 to 4-fold enhancements in the carbohydrate content, suggesting osmoregulatory role of melatonin [109]. Over expressing SNAT and HIOMT enzymes of tomato during drought, the transgenic plants overcome stress following watering, on the other hand the wild type plants died. It is well-known that exogenous melatonin increases total chlorophyll content exposed to drought [110]. Cui et al. studied that exogenous melatonin in wheat seedling regulate water balance by reducing the MDA level and this reduction in MDA by melatonin is associated with elimination of adverse effect of stress that make intact grana lamella under drought [111]. Biosynthetic gene expression of apple MzSNAT5 in Arabidopsis promotes endogenous melatonin which ultimately improves the capacity for tolerance to drought [103]. Melatonin increases photosystem II efficiency in dark and light conditions in apple trees and alleviate the photo inhibition by drought stress, thus making the leaves more efficient in maintaining the higher CO<sub>2</sub> assimilation and stomatal conductance [102]. Melatonin application enhanced the photosynthetic rate by decreasing the chlorophyll degradation and increases the activities of ROS-scavenging enzymes, and reversing the severe effects of water stress [36]. Melatonin increases the functioning of the stomata under drought exposure [77]. Melatonin downregulates an enzyme in ABA biosynthesis 9-cis-epoxycarotenoid dioxygenase (NCED), and upregulates two CYP707 monooxygenases, important enzymes involved in the metabolism of ABA on exposure to drought. The lower H<sub>2</sub>O<sub>2</sub> and ABA content in melatonin grown plants increased stomatal performance reducing the drought conditions [77].

Melatonin application prominently caused stunted growth and enabled plants to maintain uptake fluxes and also abolished the adverse effects of drought on stomatal apertures, photosynthesis, and relative water content, and it nullify the oxidative burst [112]. Melatonin application increases nitrogen metabolism enzyme such as NR, NiR, GS, and GOGAT and uptake genes that show up-regulation in the leaves under drought stress and increase uptake, utilization and N-accumulation. It has been reported that melatonin 100 µM modulate antioxidative in oat under 20% PEG-6000 stress. Melatonin upregulates mitogen-activated protein kinases expression (MAPKs) Asmap1 and Aspk11, and the transcription factor (TF) genes on exposure to drought thereby enhancing the plant's tolerance [113]. Plants efficiently regulate water balance by up-regulating the melatonin synthesis genes expression MdTDC1, MdAANAT2, MdT5H4, and MdASMT1 under drought conditions. Its treatment in *Malus* maintains the water status under drought [77]. Melatonin increase photosynthesis by inhibiting stomatal closure, increasing absorption of light energy, and inducing photosynthetic electron transport and transcription enzymes, CO<sub>2</sub> fixation was up regulated under drought [110]. Melatonin improves the water absorption in roots by regulating aquaporin channels and involved in stress mitigation [114]. Melatonin increased drought tolerance by increasing the cell turgor and water holding capacity [111]. Melatonin reduces the water deficiency by promoting antioxidants capacity and nitrate reductase in *Lupinus terminis* [115].

## 5.2. Melatonin under Salt Stress

Salinity is the most hazardous stress factor that reduces the crops production in the arid and semi-arid regions of the world [52,116,117]. A high level of salinity reduces plant growth, productivity, and seed germination, and affects the quality and quantity of the of the crop [118]. Salinity stress reduces growth attributes in the plant leaf area which then lowers the photosynthesis rate and ultimately lowers biomass production [117,119]. Exogenous application of melatonin in cotton plants relieves the negative impact salt stress [60]. Melatonin (exogenous source) was found enhancing the endogenous levels of melatonin, sugar, K<sup>+</sup>/Na<sup>+</sup>, and proline content thereby increasing the rate of germination of seeds dur-



ing conditions of salt stress. Application of melatonin increases the weight (both fresh and dry) of rice seedlings and causes enhancement in the utilization of arginine, polyamines, and nitric oxide under condition of salt stress [120]. Melatonin was also found to enhance the ATP levels, besides increasing the activity of  $H^+$ -pump [121]. Ke et al. studied the use of melatonin in minimizing the negative effects of salinity stress by accelerating polyamine metabolism and also suggested that enzyme activity can be increased that results in stimulating ROS scavenger antioxidant defenses in relation to salinity [122]. Zhou et al. found that photosynthetic process were triggered with melatonin by accelerating the protein biosynthesis and photosynthetic electron chain in tomato plants under salt stress [123]. Melatonin attenuated salt-induced decreases in relative water content, photosynthetic attributes, amino acid and antioxidant metabolism, and melatonin application improved plant performance and yield in plants [52]. Compared with the controls, application of melatonin demonstrated enhancement in the expression of antioxidant enzymes such as CAT1, APX, SOD1, Peroxiredoxin Q (PrxQ) and 2-cysteine peroxiredoxin, that resulted in an increase in the rate of photosynthesis and a subsequent decrease in oxidative damage in *Phaseolus vulgaris* (L.) grown under salt stress [124]. A similar effect of increased seed germination and growth of seedlings, antioxidants enzymes, along with reduction in oxidative damage was observed in *Medicago sativa* (L.) [125]. Melatonin enhanced salt tolerance by minimizing the sodium content in order to maintain  $Na^+/K^+$  homeostasis, it reduced lipid oxidation, and increased chlorophyll production. On the basis of metabolome profiles showing the abundances of metabolites in plants treated with salt plus metabolites. Endogenous melatonin and its intermediates having antioxidant functions indicate their role in alleviating the effect of salt stress in *Oryza sativa* [94]. Photosynthetic performance increased with melatonin under the coordinated application of salt and heat in tomato plants [15].

### 5.3. Melatonin under Low Temperature Stress

Low temperature stress negatively affects plant growth and productivity [36], which is responsible for crop loss throughout the world. Photosynthesis is the primary process affected by cold stress [126]. Cold stress reduces photosynthetic capacity, development of chloroplast, and causes a decline in chlorophyll fluorescence [56,127–129]. Melatonin supplementation in *Solanum lycopersicum* grown under cold stress helped the plant overcome damage caused by increased accumulation of ROS species, and in recovering the photosynthetic events to cope with the cold stress [130]. Different reports indicated the role of Melatonin in alleviating cold stress tolerance in *Cucumis sativus*, *Triticum aestivum* and *Oryza sativa* [55,128,131] by increasing the germination rate, and in promoting survival under extreme cold conditions in *Rhodiola crenulate* (Hook. f. et Thomson) [132]. The protective role of melatonin studied in *Vigna radiate* (L.) meristem cells of root under chilling conditions has also been studied [133]. Arabidopsis plants grown with melatonin at 4 °C have a greater root length, height, and weight [134] and upregulated cold signaling gene expression increases cold tolerance in the plants [135]. Plants grown at 6 °C showing a 2.5-fold increase in the content of melatonin when compare to plants grown at 24 °C [87]. Melatonin application at 1 mM enhanced antioxidant enzymes activity and improved plant growth and photosynthesis by minimizing oxidative stress in *Triticum* [128]. It has been observed that the reduction in proteins of PSII triggers the protective role of melatonin to PSII under cold stress [55]. The plants receiving melatonin enhanced production of ABA, and both melatonin and ABA remove cold induced oxidative damage by reducing the oxidative stress and increasing the level of AsA, GSH, and SOD, CAT, APX, and GR. Melatonin increased the expression of several cold responsive genes such as CBF and cold regulated (COR) genes [136]. Application of melatonin at 5 mol L<sup>-1</sup> helps to overcome oxidative damage caused by ROS due to an increase in the plant mineral element status and the transcript abundance of antioxidant-related genes as part of a mechanism to overcome cold stress [137]. Pre-soaking seed treatment and parental treatment with melatonin are effective ways for low temperature tolerance induction in wheat [138]. The rootstock of cucurbit

species promotes melatonin accumulation in leaves that promote MeJA accumulation and provide tolerance against cold [53].

The photoinhibition was overcome by melatonin during chilling by promoting maximum quantum yield and the effective photochemical efficiency of PS II. It induces the expression of violaxanthin de-epoxidase, and its cofactor ascorbic acid was enhanced in *Solanum lycopersicum* [95]. Furthermore, melatonin protected PSII activities via inducing antioxidant metabolism in *Oryza sativa* [56]. Photosynthetic fluorescence parameters enhanced under cold stress when plants were treated with melatonin. There was alteration in the 46 metabolites studied such as arabinose, glucopyranose, mannose, maltose, and turanose which were greatly enhanced in *Cynodon dactylon* [96]. Supplementation of 1  $\mu\text{M}$  melatonin improves growth in *Hordeum vulgare* under cold stress [139]. In a study performed on *Pistacia vera* (L.) grown under cold stress, application of melatonin caused a significant decrease in the expression of oxidative stress biomarkers, with a subsequent decrease in sugar, proline, and GABA content [140]. Melatonin treatment enhances seed germination and prevents protein and lipid oxidation in embryonic cells of *Capsicum annum* and *Zea mays*, besides causing an increase in the antioxidant levels [141,142]. Turk and Genisel reported that application of melatonin in maize plays an important role in improving plant growth attributes and in protecting plants from oxidative damage via reduction in the ROS levels [143]. In litchi fruit subjected to chilling stress, treatment by exogenous melatonin prevented discoloration of pericarp by increasing the anthocyanin levels and inducing proline accumulation [144]. In *Prunus salicina* (Lindl.) melatonin, pretreatment of fruits caused enhancement in the levels of spermine, spermidine, and putrescine via regulation of the SAMDC and TGase activities [145]. It has also been observed that melatonin increases the shelf life of sweet cherry fruits and upgrades the quality of fruit by regulation expression of different genes in *Prunus avium* (L.) [146].

#### 5.4. Melatonin under Heavy Metal Stress

Due to the setup of industries and factories, there is increased contamination by heavy elements in soil agriculture that reduce crop productivity and economy [9,10]. The Addition of heavy metals through various sources inhibits photosynthesis, alters nitrogen metabolism, growth, and yield [147,148]. The role of melatonin in heavy metal contaminated soil has been studied in the recent years [48,149]. Melatonin mitigates copper toxicity by increasing the growth characteristics and increase the mitochondrial electron transport chain resulting in the production of fewer free radical [150], and foliar application of melatonin provides cadmium tolerance in *Nicotiana tabacum* and decreases the accumulation of metal [41,58]. Heavy metal, such as Cd, Zn, and Pb-induced oxidative stress is reduced by applying 200  $\mu\text{M}$  exogenous melatonin by inducing the SOD activity in *Exophiala pisciphila* (McGinnis & Ajello) [151]. Nawaz et al., while studying *Citrullus lanatus* plants exposed to vanadium treated with melatonin, enhanced the total chlorophyll content and associated chlorophyll genes in leaves [18]. Supplementation of melatonin reverses Cd toxicity by increasing the biomass and antioxidant metabolism involved in phytochelatin biosynthesis in *Solanum lycopersicum* [152] as well as minimizes metal toxicity via improving the uptake of key nutrients such as nitrogen, phosphorus, and sulfur, and improving cell metabolism [48]. Upregulating *RsMT1* in radish confers Cd tolerance [153]. Foliar application of melatonin at 100  $\mu\text{mol L}^{-1}$  is more effective in slowing the senescence and improves seedling biomass under Cd stress in strawberry [154].

Melatonin promotes plant growth by developing antioxidant systems and alleviating heavy metal toxicity by employing its chelating property that helps in reducing their accumulation at the rhizospheric surface [155]. Lower concentrations of melatonin show a positive impact on Cd tolerance by promoting photosynthesis, growth, and maintaining relative water content and stomatal conductance through increasing proline metabolism in *Malva parviflora* (L.) [156], and preventing metal toxicity by inducing defense systems [157]. Melatonin decreases the methylation of upregulated genes *RsAPX2*, *RsPOD52*, and *Rs-GST* and scavenges lead-induced ROS in radish [158]. In a study on Indian rice cultivars,

exogenous application of melatonin overcome arsenic stress by increasing the levels of organic acids and by upregulating the expression of respiratory and sugar metabolism enzymes [159]. In *Melissa Officinalis* (L.), plants exogenous melatonin application helps to reduce oxidative damage via antioxidant defense mechanisms and, as such, contribute to a better tolerance to Zn and Cd [160]. Improving plant growth and minimizing oxidative damage via development of the antioxidant system on application of melatonin exogenously contributes to increasing the yield among chromium stressed *Triticum aestivum* [161]. Melatonin application in *Brassica napus* helps to overcome the effect of Al and Cd stress by causing enhancement in the antioxidant armor and in overall plant growth [162]. Application of melatonin helps in reducing the uptake of Pb from the soil; thereby contributing to enhancement in the plant biomass, GSH content in leaves, and antioxidant defense in *Carthamus tinctorius* [163]. A recent study reported an improvement in regulating the enzymes of photosynthesis that contribute to growth in *Eruca vesicaria* (L.) plants growing under Pb stress [164]. Melatonin (50 or 100  $\mu\text{M}$ ) attributes to physiological parameters of leaves and overall growth. Its decrease in ROS and triggering of NO production contributes significantly to overcoming growth of *Triticum aestivum* grown under Cd-stress [71].

### 5.5. Melatonin under Herbicide Stress

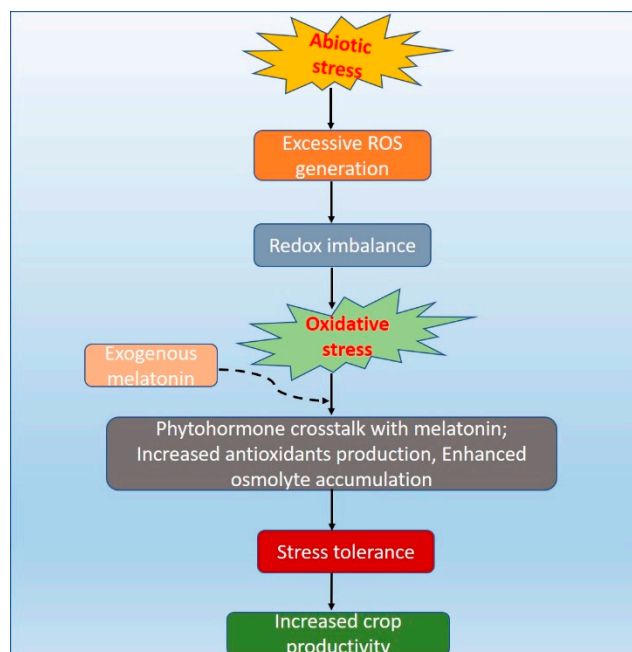
Herbicides are applied in crop fields to increase their yield. These herbicides remain in the soil for a longtime affecting the next crop or even the plants used as green manure. Presently, these herbicides are chemical agents mostly employed for the check growth and development of weeds in the agricultural field and their use in high concentration inhibits physiological function in plants [165]. Use of commonly used herbicides in agriculture effects both the target and other associated plants [166,167]. Their use in high concentrations inhibits plant physiology [165]. Use of herbicides such as pendimethalin on *Foeniculum vulgare* (Mill.) leaves [168]; chevalier in *Triticum aestivum* cultivars [169] and in *Vicia faba* (L.), cause a decrease in photosynthesis [170]. Application of a 10 mM dose of glyphosate reduced photosynthesis-related proteins in *Zea mays* [171]. In *Triticum aestivum*, a reduction in chlorophyll content was reported with 300  $\mu\text{gkg}^{-1}$  chlorimuron-ethyl [172]. Numerous Research publications have reported the role of melatonin in minimizing the adverse effects of herbicides applied to plants. Kaya and Doganlar studied the effects of the herbicide pendimethaline (Pend) and drought stress on pepper. Melatonin at 50  $\mu\text{M}$  alleviated adverse effects of 10% PEG and herbicide pend (8, 16 and 32 mM) stresses by promoting the antioxidant enzyme, relative water content, photosynthetic pigments, proline, and mRNA levels [92]. Melatonin increased P5CS expression and the enzymes involved in proline biosynthesis, on exposure to Methyl viologen [173]. Melatonin pretreated seeds decreased oxidative stress in growing seedlings. This beneficial effect was reported in leaves where their reduced accumulation of superoxide anion and protection of photosynthetic attributes under paraquat in *Pisum sativum* [93]. Liu et al., reported in *Cucumis sativus* that melatonin addition could relieve oxidative stress induced by imidacloprid via its degradation through increased antioxidants such as AsA/DHA, GSH/GSSG ratios, MDHAR, DHAR, and GR, maintaining the ascorbic acid-glutathione cycle [174]. Growth of *Ipomoea batatas* (L.), in MS media supplemented with a combination of bentazon and melatonin helped in reducing the effect of bentazon [175].

### 5.6. Melatonin under Temperature (High) Stress

Environmental stressors, such as extreme temperatures, can cause severe damage to plants. High temperatures hinder plant growth and yield, and thus pose a threat to growth potential and food security [26,57,176,177]. Heat stress changes the stability of proteins and cause changes on the enzyme level, as well as biomolecules which are associated with the generation of ROS [27,78]. Higher temperatures disrupt the fluidity of the membrane and activities of enzymes [79], leading to a reduction in photosynthesis, growth, and yield [27,40].

High temperature application increases the level of melatonin in *Solanum lycopersicum* [57] suggesting melatonin's role in the defense against heat stress. Rising temperatures increase melatonin levels suggests its power to increase heat tolerance in green micro-algae *Ulva* sp. [178]. Supplementation of melatonin reverses the ill effect of high temperature on photosensitive and thermosensitive *Phacelia tanacetifolia* (Benth.) seeds [179]. Melatonin exposure enhanced the percentage of germination in heat stressed seeds by 60% in *Arabidopsis thaliana* because of its strong antioxidant metabolism activity [180]. Melatonin deficiency at the endogenous level induces oxidative stress as revealed by high MDA concentration and high electrolyte leakage in tomato plant leaves grown in high temperatures. Furthermore, there is a reduction in ascorbate peroxidase and catalase activity that play an important role in thermotolerance [181]. Exogenous application of melatonin (100  $\mu$ M) helps in increasing the levels of endogenous melatonin, which contributes to enhancement in the expression of photosynthesis-related genes and, as such, activity of PSII in tomato plants [57]. Melatonin applied to *Lolium perenne* L. not only increased melatonin and cytokinin endogenously, but also reduced the concentration of ABA under heat stress [65], protected proteins from misfolding, and oxidizing under heat stress in tomato plants [182]. Melatonin maintains proper redox signaling preventing oxidative stress in *Cucumis sativus* [183]. Reports show that melatonin increases antioxidant enzyme activity in tomato pollen on exposure to heat stress [184]. Exogenous melatonin more effectively increased the biosynthesis of enzymes related to nitrogen metabolism, nitrate content, and restricting the ammonium accumulation in cucumber seedlings at high temperatures, thus providing resistance [185].

Foliar application of melatonin at 10  $\mu$ M reduced heat induced photoinhibition by over expressing the *N*-acetyl serotonin methyltransferase (ASMT) gene. This was achieved by minimizing the electrolyte leakage through enhancing the photosystem II and high temperature tolerance in tomato seedlings by increasing the antioxidant defense system [182]. Table 1 shows abiotic stress-induced changes on exposure to melatonin in plants. Mechanisms of abiotic stress induce oxidative stress and the role of melatonin in overcoming the stress is shown in Figure 2.



**Figure 2.** Role of melatonin in overcoming abiotic stress.

## 6. Melatonin Crosstalk with Phytohormones under Abiotic Stresses

Research has shown that coordination between melatonin and NO as a signaling molecule performs many actions in plants such as growth and abiotic stress tolerance [186].

Metabolites that are enhanced are carbohydrates such as fructose, galactose, glucose, sucrose, and proline that are important components of osmotic adaptation in abiotic stress response [96]. The regulation of rice melatonin-related genes by jasmonic acid (JA), abscisic acid (ABA) in response to numerous stresses demonstrate the mechanism of crosstalk of ABA and JA. Melatonin is reported to enhance the contents of polyamine by increasing the metabolic flow from arginine and methionine to polyamines. Melatonin also decreased off salt-induced degradation of polyamines [122]. SA and melatonin share the common biosynthetic precursor and reduce the damage caused by water deficits. The proper utilization of these molecules is responsible for promoting plant development and crop yield [58]. Melatonin upregulates the expression of genes in GA biosynthesis, downregulates important genes in ABA biosynthesis, and upregulates ABA 8'-hydroxylase genes, which mediate the changes in ABA and GA levels during germination [49]. MeJA increases the accumulation of melatonin, causing the formation of a self-amplifying feedback loop that is involved in cold tolerance [53] as well as increasing the biosynthesis of metabolic enzymes of auxins, brassinosteroids, and NO generation, and its associated expression of genes that have a role in defense [149]. Salt stress recovers amino acid constituents by applying melatonin to the roots, except Proline on the 8th day. After 8 days, the highest value for glutamic acid and lowest value was seen for cystine in salt treated plants exposed to melatonin. A reduction in ABA content and an increase in the content of salicylic acid is studied in salt treated plants with melatonin [52]. Melatonin promotes endogenous melatonin and inhibits the NCED1, an ABA synthesis gene, as well as up-regulates ABA catabolic genes, ABA8ox1 and ABA8ox3, decreasing the accumulation of ABA by promoting the stomatal reopening [53]. Melatonin has similar actions to those of indole-3 acetic acid [73] in that it induces endogenous NO that regulates transcription factors and maintains redox homeostasis involved in stress tolerance [187]. Exogenous application of melatonin at 0.1  $\mu$ M melatonin increased root elongation, increased endogenous IAA levels in the root, while as treatment with 100  $\mu$ M indicating inhibition on root growth had no effect on IAA in *Brassica juncea* [34]. Melatonin under drought stress induces the function of stomata by maintaining the balance of water and downregulating the ABA pathway in *Malus hupehensis* [77]. Melatonin and salicylic acid are involved in abiotic stress tolerance as these both share common biosynthetic pathways [58]. Melatonin increases GA content but reduces ABA content when exposed to high temperature stress highlighting its antagonistic role in the developmental processes [57]. The crosstalk of melatonin with different signaling molecules revealed a relation in their biosynthetic pathways.

It has been reported in *Cucumis melo* (L.) that melatonin regulates linoleic acid metabolism and promotes root development. Melatonin interacts with Jasmonic acid and inhibits the expression of LOX-related genes to relieve against oxidative stress [188]. Melatonin and NO interacts with each other in inducing plant growth and develops tolerance to abiotic stress through inducing the antioxidant system [189]. Melatonin induces either NO production or its scavenging activity, and enhances the activity of NOS-like proteins [190,191]. As revealed by the RNA sequencing method, melatonin induced the seed germination in correlation with auxin, gibberellin (GA), and abscisic acid (ABA) in *Arabidopsis* [192]. Melatonin is involved in inducing seed germination by counteracting ABA to maintain the ABA/GA<sub>3</sub> balance [193]. Exogenous melatonin also induces the production of endogenous NO which antagonizes ethylene biosynthesis and, henceforth, delays senescence [194]. Melatonin, along with H<sub>2</sub>S, helps in mitigating high temperature stress by improving photosynthetic attributes and carbohydrate metabolism [64]. Besides reducing accumulation of indole-3-acetic acid, melatonin (20  $\mu$ M) application in *Oryza sativa* grown under fluoride stress hinders fluoride uptake and alters the phytohormone homeostasis [72]. ABA enhanced relative water content of drought treated leaves by minimizing the water loss, melatonin was found increasing it by inducing the water uptake efficiency. Additionally, ABA and melatonin were found capable of modulating activity of superoxide dismutase under drought stress [195]. Melatonin application in the rhizosphere imparts greater protection than its foliar application under conditions of drought stress.

Concentrations of salicylic acid and jasmonic acid in the root zone were significantly high for foliar application of melatonin in soybean [196]. Increased photosynthesis, reduction of ABA, and lowering of ROS induced by drought are key attributes of the role played by melatonin.

### 7. Photosynthetic Regulation by Melatonin under Abiotic Stress

Photosynthesis is the process in plants which is restricted to the green parts of plants i.e., leaves [197]. Photosynthesis controls numerous metabolic processes and converts light energy into chemical energy [198,199]. Both the light and dark reactions of photosynthesis occur in chloroplast, which is highly sensitive to abiotic stresses. It has been shown that melatonin application increased photosynthesis under abiotic stress [56,95]. Melatonin improves photosynthesis and maintains redox status in a dose-dependent manner in *Brassica juncea* [200]. Recently, it has been studied that melatonin triggers endogenous melatonin, through the Phyto-melatonin receptor CAND2/PMTR1. An increase in endogenous melatonin levels then leads to an increase in photosynthesis, and the promotion of the biosynthesis of hormones, nitric oxide, and polyamine [48,201]. However, very recently, it has been reported that the application of melatonin reduced ROS production by creating a constant flow of electrons, thereby maintaining the abundance of *PsbO* and *D1* for improving the repair of photosystem II [202]. Melatonin plays a crucial role in photosynthesis and photoprotection [104]. Melatonin induces chlorophyll content and biomass, and increases the efficiency of the reaction centers of photosystem II in the macroalga *Ulva* sp. under salt stress [178] and in the freshwater *Chara australis* (L.) [203]. Generally, plants under stress conditions close their stomata to prevent water loss, so affecting stomatal conductance and reducing photosynthesis [8]. However, melatonin increases the stomatal function and permits the reopening of the stomata in plants treated with salt [91], and hence, improves the net photosynthetic rate of plants under salt stress. Melatonin treatment improved the Fv/Fm by promoting the chlorophyll biosynthesis under salt stress [49]. Melatonin expressed photosynthesis-related genes under salt stress and had a positive impact on glucose and fatty acid metabolism, and ascorbic acid synthesis in *Cynodon dactylon* [89]. Moreover, melatonin enhanced the transcription level of photosynthesis-related genes under salt stress and protected the photosynthetic apparatus [88]. Reports suggest that, under drought stress, melatonin can directly scavenge ROS and improve the antioxidant activity of enzymes to remove the oxidative damage induced by drought stress in cells [36]. Recent work on melatonin has also suggested the beneficial role of melatonin in improving plant photosynthetic rates under water stress [204] by inhibiting chlorophyll degradation in Barley roots [205].

The photosynthetic performance of plants enhanced by melatonin protects chlorophyll molecules and the chloroplast ultrastructure of plants treated with drought stress [206,207] and regulates photosynthesis by expressing the key gene involved in chlorophyll metabolism in *Carya cathayensis* (L.) [208]. The increased leaf area in plants treated with melatonin was also involved in improving photosynthesis under water-deficit conditions in *Coffea arabica* (L.) [209]. Melatonin in mesophyll cells maintain the cell turgor and water balance to induce the stomatal conductance and chlorophyll fluorescence in *Medicago sativa* [210]. Melatonin induces the pathway of carbon fixation by modulating the expression of important enzymes [83]. The ROS disrupts PSII due to oxidative stress on the thylakoid membrane [211] and the use of melatonin reduces ROS by preventing the damage to thylakoid and chloroplast membranes in *Fagopyrum tataricum* (L.) [212]. Melatonin induces the activity of Calvin cycle enzymes and protects PSII proteins under cold and drought stress, respectively [50,56]. Melatonin recovers gas exchange and chlorophyll content on exposure to salt stress in *Brassica juncea* [50,52].

### 8. Conclusions

Abiotic stresses cause various problems at the physiological and molecular levels in plants, resulting in a significant reduction of productivity worldwide. Melatonin is a

bioactive compound in a number of vascular plants. The aim of the current review was to collect the research completed in the recent year on melatonin under different abiotic stresses. There has been a surge in research publications on this topic in the last few years. Crosstalk between auxin and melatonin should be focused on more as both share the common precursor: tryptophan. Exogenous melatonin recovers plant vigour and growth under different stresses. Based on the literature in the text, it may be concluded that melatonin is involved in combating the numerous stresses via regulating the antioxidant metabolism and protecting the photosynthetic machinery. Increased photosynthesis makes it easier to improve the crop productivity and thus address the key issue of food insecurity around the world. As abiotic stress reduces the quality and yield of crops, the application of melatonin at a field level can be useful from an agronomic point of view. Future research is required to know the genetic mechanisms and metabolic pathways involved during recovery under stress conditions on exposure to melatonin. Future studies using phytohormone mutants are needed to clarify how melatonin functions with various phytohormones in different physiological processes and crosstalk with more signaling molecules is to be elucidated. Melatonin was shown to influence field crops and also has been proven beneficial in increasing the yield of crops and nutraceutical values. Melatonin-rich plants could be used to recover soil contaminated with chemicals and improve the phytoremediation practices. Detailed research should be conducted on molecular aspects using Omics approaches to figure out gene regulating physiological, biochemical, and anatomical features in response to melatonin under abiotic stress. Melatonin is a nontoxic biodegradable molecule which could be used for promoting organic farming [213]. Use of synthetic melatonin, a cheap compound, or phytomelatonin-rich extracts, should be a key strategy in improving the plant tolerance against abiotic stress [214,215].

**Author Contributions:** Conceptualization, A.T.J. and M.A.; writing—original draft preparation, A.R. and A.K.M.; writing—review and editing, T.S.P.; M.H.; A.T.J. and M.A.; Data for Table, A.F. and T.S.P.; Figure preparation, A.T.J. and M.A.; supervision, A.T.J. and M.A.; project administration, M.A.; funding acquisition, A.K.M. and M.A. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by UGC and SERB New Delhi, India, with grant numbers 30-441/2018 and SRG/2019/001766.

**Institutional Review Board Statement:** Not Applicable.

**Informed Consent Statement:** Not Applicable.

**Data Availability Statement:** Not Applicable.

**Acknowledgments:** Authors acknowledge all colleagues whose comments helped in increasing the readability of contents and information given under different headings.

**Conflicts of Interest:** The authors declare no conflict of interest.

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