South African Journal of Botany 159 (2023) 179–190

Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

Linking the role of melatonin in plant stress acclimatization

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ARTICLE INFO

Article History:
Received 14 February 2023
Revised 22 April 2023
Accepted 22 May 2023
Available online xxx

Edited by: Dr K.R.R. Rengasamy

Keywords:
Melatonin
Abiotic stress
Antioxidants
Reactive oxygen species
Biotic stress
Biotechnology tools
Stress protectant

ABSTRACT

Melatonin is a derivative of tryptophan and consists of a conserved domain present ubiquitously from bacteria to higher organisms. Melatonin is an emerging pleiotropic plant growth hormone that is pivotal in coping with various biotic and abiotic stress conditions. It regulates downstream signaling transduction that modulates plants' physiological and biochemical pathways. Melatonin can be externally applied and could strengthen the stress tolerance mechanism of plants by enhancing ROS-scavenging enzymatic and non-enzymatic antioxidant defense systems. Which consequently exhibits lower lipid peroxidation, MDA content, greater enzyme activity, metabolic pool, ion homeostasis, and plasma membrane integrity under stress conditions. In addition, melatonin protects photosynthetic machinery by maintaining cell membrane stability and chlorophyll recovery. It also stimulates the electron transport chain during photosynthesis and D1 protein biosynthesis and maximizes the photochemistry efficiency (Fv/Fm) of photosystem II and photochemical quenching. Besides abiotic stress, melatonin plays a significant role in biotic stress tolerance. This review emphasizes Melatonin as a stress protectant under biotic and abiotic stress. Further, we have highlighted integrating advanced biotechnology tools with recent information for the possible application of melatonin in the current scenario of changing climate.

1. Introduction

Melatonin (MEL) is chemically N-acetyl-5-methoxy-tryptamine, a biogenic indoleamine compound and a growth regulator or biological modulator with diverse functional dimensions. It was first discovered in 1958 by Lerner et al. in the bovine pineal gland. In 1988 it was found in the unicellular photosynthesizing algae *Lingulodinium polyedrum* and in 1993 in the Japanese morning glory (*Pharbitis nil*) plant. Compared to animals, plants contain significant amounts of melatonin, known as phytomelatonin (Blask et al., 2004). In Plants, approximately 140 different species have been documented and quantified for the presence of melatonin in various parts such as roots, shoots, leaves, fruits, and seeds (Posmyk and Janas, 2009; Posmyk et al., 2008). The MEL is also reported in several horticulture fruit crops, including strawberries, bananas, berries, kiwis, pineapples, apples, and grapes, as well as tart cherries (Manchester et al., 2000) and tomatoes in differential quantities (Van Tassel and O'Neill, 2001). The most abundant melatonin is observed in seeds and leaves, while the least is found in fruits (Manchester et al., 2000; Burkhardt et al., 2001; Van Tassel et al., 2001). Toxic levels of this indoleamine are present in the Poaceae family plants such as rice, tall fescue, and wild perennials such as *Hypericum perforatum* (L.). *Datura metal* L. flower buds had significant levels of this chemical, which was dropped during flower development. MEL concentrations in higher plants are estimated in the picogram-to-nanogram range per gram of tissue (Kolar and Machackova, 2005). Also, seeds of plants have different quantities of MEL for example, Pistachio (*Pistacia vera*) kernels have the highest amounts of melatonin, but potato tubers are devoid of it. According to recent research, plants are speculated to manufacture endogenous melatonin. Many plants, such as herbs, crops, fruit trees, and others, produce melatonin, which is assumed to be generated in the mitochondria and chloroplasts (Boccalandro, 2011). This indicates the presence of MEL in different plant parts endogenously, which could be manipulated through biotechnological tools to provide stress tolerance.

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https://doi.org/10.1016/j.sajb.2023.05.034

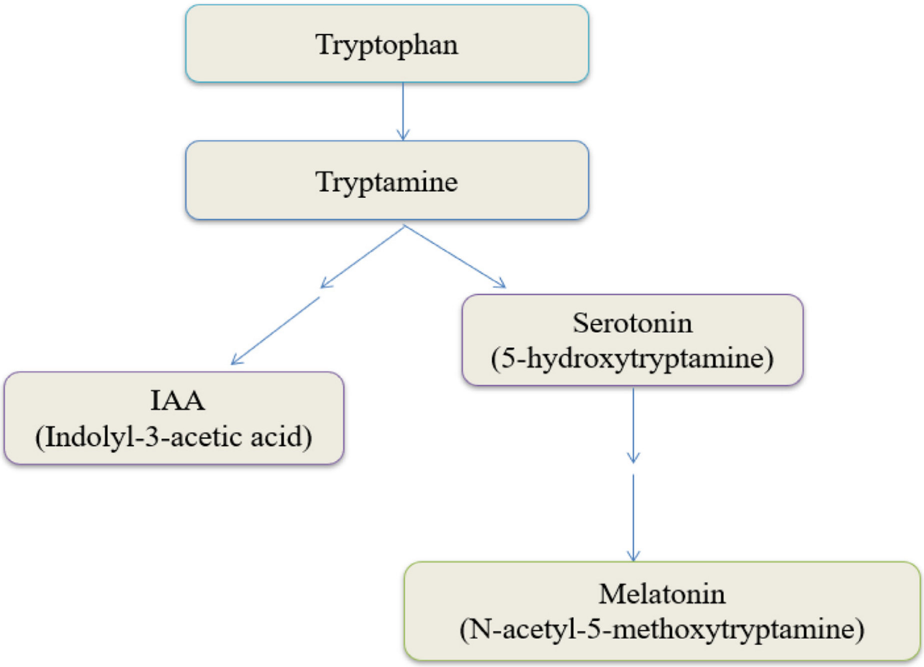

Fig. 1. Molecular structure of melatonin and its related compounds in the biosynthesis pathway: tryptophan, serotonin, and tryptamine. This last compound is a precursor of the auxin indolyl-3-acetic acid, IAA.

MEL's structural similarity with Auxin (IAA) enables botanists and researchers to study deeper and point out its role as a regulator for plant growth and development (Hernandez-Ruiz et al., 2004; 2005; Arnao and Hernández-Ruiz, 2015). Therefore its biosynthesis, transport, conjugation, receptors, physiological effects, and signal transduction chain must be explored (Chen et al., 2018) to highlight its role as a plant hormone. MEL biosynthesis starts from the serotonin generation from the tryptophan, which is then converted to melatonin by different enzymes (Mannino et al., 2021). Interestingly both melatonin and auxin share a common biosynthetic pathway through the precursor tryptophan, which is further helpful in generating tryptamine and IAA produced by indole-3-acetaldehyde-in the tryptophan-dependent IAA biosynthetic pathway (Fig. 1). This suggests that these phytohormones may share some similarities in their multifunctional activities in plants.

MEL impacts and regulates plants' physiological and biological processes, including signal transduction and phytohormonal crosstalk. These activities as plant stimulators include seed growth, root formation, and plant development as a stress protector, which enhances plant performance during stress conditions (Wang et al., 2016; Tan and Reiter, 2019). Auxin, cytokinin, and gibberellin, which encourage plant development, increase polyamine content in plant tissues. At the same time, inhibitory hormones (abscisic acid and ethylene) lower it, suggesting MEL may have a physiological role in plant growth and development. Further studies confirmed MEL's role in regulating seed germination, organogenesis, root development, biomass production, circadian rhythms, sexual behavior (Hardeland et al., 2012), as well as membrane integrity (Zhang et al., 2012; Tan et al., 2012; Zhang et al., 2014; Weeda et al., 2014, Lee et al., 2015; Qian et al., 2015; Cai et al., 2017).

This pleiotropic molecule is biodegradable and nontoxic to humans (Zhang et al., 2012). Since it has the amphiphilic or amphipathic molecular character to move freely across the body to any aqueous section or vasculature, it has immense field application for crops. When the plant is exposed to abiotic or biotic stress or perceives MEL, it modifies and swiftly upregulates the activity of several antioxidant enzymes and stress-tolerance-associated genes and activates downstream signaling transduction pathways. Therefore primarily acts as an antioxidant or phyto-protectant and can address climatic challenges like heat, drought, and cold, as well as pathogen attacks. This review aims to provide an overview of recent developments in the study of Phytomelatonin roles in stress regulation, mechanism, and cellular redox signaling, cross-talk with other phytohormones, and biotechnological intervention to tackle future crop science problems Fig. 2.

2. MEL: emerging stress protectant

2.1. Role in abiotic stress

Arid and semi-arid regions are more vulnerable to abiotic stresses due to global warming, widening rainfall disparities, and poor drainage (FAO, 2005; Kijne, 2006; Zhang and Shen, 2017). Drought stress intensity and duration affect the transition from one developmental stage to the next and the specific developmental phases where drought stress manifestations arise. Because drought impacts the plants' vegetative growth and causes them to flower earlier, their growth period is shorter, and their yield is lower. Additionally, drought has several detrimental impacts on plants, including reduced relative water concentration, decreased water potential in leaves, loss of turgidity, and reduced cell size, all of which lead to reduced photosynthetic pigments, metabolic disturbances, and, eventually, plant mortality. External application of MEL in crops such as coffee, maize, flax, alfalfa, moringa, etc., provided tolerance against drought by ROS induction, induction of chlorophyll biosynthesis, and chloroplast structure protection. MEL-priming improves drought tolerance in maize seedlings by alleviating the negative effect of ROS (Muhammad et al., 2023). The negative effects of waterlogging were mitigated by spaying melatonin on the leaves of sorghum. Notably, its exogenous foliar spraying enhanced the chlorophyll content and improved the maximal quantum yield of photosystem II photochemistry (Fv/Fm), resulting in higher rates of photosynthesis. In addition, it markedly decreased the malondialdehyde (MDA) content by upregulating antioxidant enzyme activities (Zhang et al., 2021). The detailed role of MEL in abiotic stress tolerance in different crops is represented in Table 1.

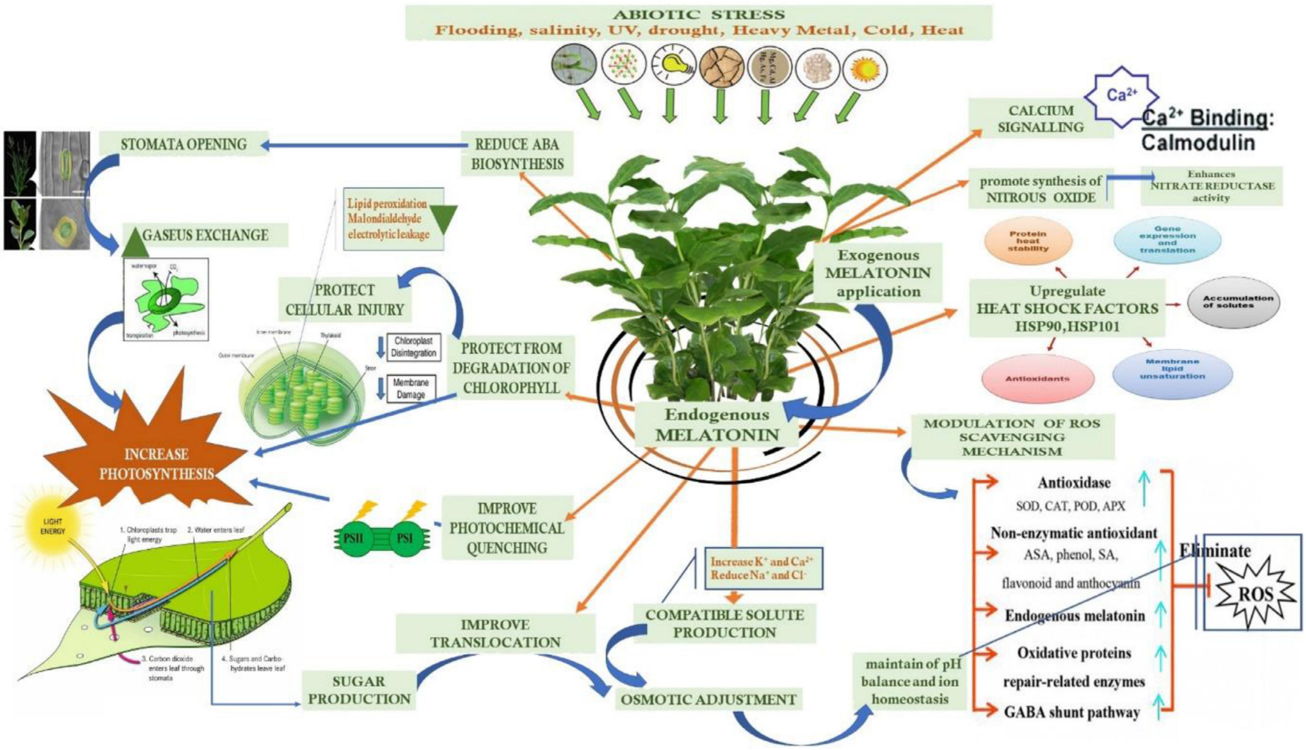

Fig. 2. Overall performance of melatonin under abiotic stress for enriching stress tolerance.

Temperature increase (5 °C) above the optimal growth temperature causes three types of damage; oxidative stress caused by ROS; dicarbonyl stress induced by methylglyoxal, which reacts quickly with biomacromolecules; cell dehydration or desiccation due to a water deficit caused by osmotic stress; and loss of biomembrane integrity are the most common effects. These changes in optimum growth temperatures significantly impact plant enzyme activity and membrane fluidity, altering plant development and growth and decreasing yield. Heat stress-induced endogenous MEL hormone production and increased anti-oxidant capacity improve the plant thermo-tolerance (Liang et al., 2018; Ahamed et al., 2019). For example, rice under heat stress showed increased melatonin synthesis, which might indicate its functions in heat tolerance. Melatonin increases photosystem II performance when applied exogenously Because it reduces energy loss, light absorption, photosynthetic pigment content, and electron transport rate. Under heat stress, MEL administration significantly improves thermo-tolerance by reducing ROS, electrolyte leakage, and malondialdehyde levels. A considerable increase in antioxidant enzymes such as SOD, POX, and CAT was observed in response to external MEL treatments. Also, some non-enzymatic antioxidants, such as vitamins C and E, were increased, reducing ROS concentration and lipid peroxidation under high temperatures (Yu et al., 2022). MEL may also help photosensitive and thermosensitive *Phacelia tanacetifolia* Benth seeds to overcome the inhibitory effects of light and high temperatures (Tiryaki and Keles, 2011). Compared to the control, MEL treatment also boosted the germination percentage of heat-stressed *Arabidopsis thaliana* seeds by 60 percent; this effect was likely caused by the MELs high antioxidant activity (Yang et al., 2021). Plants are exposed to oxidative stress due to high temperatures, which causes lipid peroxidation and membrane damage, as well as the breakdown of proteins, enzyme inactivation, color bleaching, and DNA strand disintegration. MEL protects tomato seedlings from heat stress by regulating redox potential and polyamine and nitric oxide production (Jahan et al., 2019). When exposed to heat stress, MEL also helps increase the activity of nitrogen metabolism enzymes, which increases nitrogen content while lowering ammonia levels (Jahan et al., 2021).

Melatonin-mediated heat stress responses are mediated by heat shock factors, master mediators for heat-responsive genes. HSFA2 (Heat shock proteins A2s) and Heat-stress associated HSA32, as well as HSP90 and HSP101, have contributed to Arabidopsis melatonin-induced thermotolerance (Shi et al., 2015). HSFA1 genes are highly expressed in response to high-temperature stress, a unique feature of thermo-tolerance (Liu and Charng, 2012). Interestingly, MEL biosynthetic gene (ASMT) overexpression has similar effects. Also, melatonin-treated or ASMT-overexpressing plants had little ubiquitinated protein aggregation during heat stress, suggesting its protective role in heat stress. MEL pre-treatment and overexpression also increased transcript levels of heat shock protein genes and autophagy-related genes under heat stress. MEL protects tomato cellular proteins from heat stress by triggering HSPs and autophagy, which refold or destroy damaged proteins (Jahan et al., 2021). Interestingly, the amount of AsA and the activity of various antioxidant enzymes increased after MEL treatment. To go along with this increase in activity, researchers have found increases in enzymes associated with the AsA-GSH cycle, such as APX, MDHAR, DHAR, and GR (Khan et al., 2020). Also, MEL treatment raises the expression of 28 glutathione S-transferase genes, reducing the oxidative damage created under heat stress (Jahan et al., 2021).

Low temperatures have also been linked to damage to cell membranes, which impacts the synthesis of sugars, phenolics, phospholipids, proteins, and ATP (Zhou et al., 2014). When the temperature is low, plant cells overproduce ROS compounds such as superoxide radicals ($O_2.$), H_2O_2, and hydroxyl radicals (OH-). ROS can cause lipid peroxidation and protein and nucleic acid oxidative changes (Sharma et al., 2012). Physiological and metabolic effects of cold stress on cell dynamics include membrane damage, ETC interruptions, a high amount of ROS formation, and imbalanced ion homeostasis, among others. Both temperature extremes hamper seed germination, further enhancing the damage caused by pathogens and ultimately resulting

Table 1
Role of melatonin in inducing different abiotic stress in various crops plants.

Crops	Types of stress	Application of MT	Effects of MT	Refs.
Cotton	Salinity stress (150 mM)	20 μM	Enhanced germination and hypocotyl length	Chen et al. (2021)
Soybean	Salinity stress (100 mM)	0.10 mM	Increased chlorophyll synthesis, upregulates antioxidant defense mechanism and reduced electrolyte leakage	Alharbi et al. (2021)
Sugar beet	Salinity stress (600 mM)	100 μM	Increased seedling growth, root yield sugar contents and chlorophyll contents, efficacy of PS-II is increased, maintenance of $Na^+$and K^+ionic balance and removal of H_2O_2 from cell	Liu et al. (2022)
Oat	Salinity stress (150 mM)	100 μM	Reduced H_2O_2 and MDA accumulation and increased chlorophyll content, leaf surface area, APX, CAT, POS and SOD upregulation of genes	Gao et al. (2019)
Tomato	Salinity and drought (150 mM)	150 μM	Reduced ROS production, efficient functioning of PSII and increased activity of antioxidant enzymes	Samanta et al. (2021)
Coffee	Drought stress (40% reduced water content in field)	100 μM	Decreased chlorophyll degradation and electrolyte leakage, increased activity of CAT and SOD and upregulation of gene AREB encoding ABA responsive elements	Cherono et al. (2021)
Maize	Drought stress (40% reduced water content in field)	100 μM	Increased Biomass accumulation by decreasing ROS production, increased photosynthesis and enhanced activities of APX, CAT and POD	Ahmad et al. (2021)
Flax	Drought stress (50% reduced water content in field)	7.5 mM	Improvement in growth, photosynthetic efficiency, Auxin content, soluble sugar and activities of CAT and POD was increased	Sadak and Bakry (2020)
Alfalfa	Drought stress imposed by withholding water for 7 days	10 μM	MDA accumulation was reduced. ROS activity decreased due to higher activities of APX, CAT, GR and SOD enzymes	Diatta et al. (2021)
Moringa oleifera	Drought stress (Skipped irrigation at 45 and 60 days after sowing of crop with 50% and 40% of field capacity)	150 μM	Improved growth, yield and photosynthetic pigments, phenols, IAA concentration and reduced MDA accumulation and decreased ROS production due to higher expression of APX, CAT and SOD genes	Sadak et al. (2020)
Wheat	Heat stress (40 °C)	100 μM	Reduces oxidative damage by decreasing H_20_2 concentration and enhances activity of antioxidant in plant	Buttar et al. (2020)
Pistachio	Chilling stress (-4 °C)	100 μM	Reduced H_2O_2 and MDA accumulation electrolyte leakage, chlorophyll degradation and activities of APX and GSH	Barand et al. (2020)
Tea	Chilling stress (-5 °C)	100 μM	Increased photosynthetic rate and reduced ROS accumulation due to high antioxidant activity	Li et al. (2019)
Barley	Chilling stress (4/2 °C day/night temperature)	10 mM	Increased activity of antioxidant, high photosynthetic activity and efficient electron transport chain	Yang et al. (2022)
Water melon	Heavy metal stress (50 mg/L Vanadium stress)	Trace quantity	Increased chlorophyll synthesis, photosynthesis efficiency increased and enhanced SOD and CAT activity was observed	Ul Haq et al. (2021)
Cucumber	Heavy metal stress (30 μM lead stress)	150 μM	Increased leaf surface area, chlorophyll content with improved photosynthetic rate, improved stomatal conductance, high transpiration rate, PSII activity was improved under Cd stress	Uzal et al. (2023)
Tobacco	Heavy metal stress (15 μM lead stress)	200 μM	DNA Damage protection from lead induced heavy metal stress, increased antioxidant activity and reduction in death of cells	Kobylińska et al. (2017)

in plant mortality. The application of MEL can control these damages. For example, high endogenous MEL level in Pistachio kernels helps the plant to withstand temperatures ranging from 10 to 48 °C without succumbing. Also, plants such as cacti, sage, marigolds, lilies, and willow trees (Chilopsis) may have high melatonin levels to withstand extreme temperatures (Reiter et al., 2015). It also implies that melatonin concentrations are related to regional distribution. Thus, plants that ordinarily grow at very high latitudes might also have higher levels of MEL to help them survive in freezing temperatures (e.g., plants growing on the tundra). Carbon fixation is also hampered by the accumulation of cold-generated ROS, inhibiting the Calvin cycle's enzyme regulators (Ding et al., 2017). Cold-induced nonuniform seed germination reduced seedling vigor, and late ontogenic development in horticulture crops was mitigated through MEL treatment (Ding et al., 2017). MEL primarily induces the antioxidant enzyme activity of glutathione reductase, superoxide dismutase, and ascorbate peroxidase, countering the adverse effects of oxidative stress (Li et al., 2017b). Exogenous MEL treatments reduce photoinhibition and improve nonphotochemical quenching/NPQ (Fv/Fm) by activating violaxanthin de-epoxidase activity under chilling stress. MEL treatment considerably lowers NPQ, which protects the photosynthetic system and cell membranes from cold-stress damage peroxidation of the lipid bilayer. It reduces electrolyte leakage by inhibiting the development of membrane-stabilizing enzymes like lipoxygenase and phospholipase D (Ding et al., 2017). Reduced peroxidation of lipids in tissues increased antioxidant enzyme activity, which improved seed germination. Under chilling stress, MEL treatments reduced H_2O_2, MDA, and ABA levels but boosted SOD and CAT enzyme activity (Wang et al., 2016). In addition to antioxidant enzyme activation, MEL was effective because secondary metabolites such as sucrose, amino acids, alcohols, and organic acids, and putrescine and spermidine production were enhanced in high quantities (Rehaman et al., 2021). MEL's induced antioxidant and redox homeostasis capacity aids in the reduction of morphological alterations brought on by cold stress. As a result, phenol build-up and 2,2-diphenyl-1-picrylhydrazyl (DPPH) radical scavenging activity is increased when exposed to low temperatures. Low temperatures also promote GABA shunt and phenol propanoid pathways (Ma et al., 2021). It was found that treating *A. thaliana* plants with melatonin-activated cold response genes such as CBF transcription factors (C-repeat-binding factors), Cold-Regulated 15A, and CAMTA1 (Calmodulin-Binding Transcription Activator 1), which are necessary to induce transcription of antioxidant zinc-finger protein genes ZAT10 and ZAT12 in the plants (Qari et al., 2022). Melatonin appears to play a role in the expression regulation of a wide range of genes implicated in the cold response, according to the information currently available (Bajwa et al., 2014).

Similarly, excessive Na^+ generation in salinity stress disrupted ion homeostasis in the cytosol, inhibiting the growth and development of plants. Excessive salt-ion concentrations are transported from the cytoplasm into vacuoles or compartmentalized into distinct tissues to maintain cellular homeostasis (Singhal et al., 2021). Salinity stress is a devastating abiotic stress limiting global crop output on at least 20% of irrigated land (Kader, 2010; Chhabra and Kamra, 2000). Salt affects approximately 800 Mha, around 6% of worldwide land coverage (FAO. 2008). It also affects 32 mha (2%) of the 1500 million ha of dryland agricultural land. According to current estimates, 45 Mha (20%) of the total irrigated land across the globe is salt-affected (FAO, 2008). The two primary ways salt stress affects plants are osmotic and ionic toxicity. A lack of water and oxidative stress is caused by soil salinity, which, in turn, suppresses plant growth. High salinity disrupts physiological and biochemical processes such as photosynthesis, nitrogen metabolism, ion homeostasis, antioxidant phenomena, and plant osmolyte build-up. These disturbances cause cell death (Munns 2005; Rozema and Flowers 2008; James et al., 2011; Rahnama et al., 2010., Agarwal et al., 2013; Pompeiano et al., 2016). Cell death occurs when the cellular membrane is destroyed by osmotic stress and the excessive ROS generated from it. Plants must maintain low Na+ concentrations and high cytosolic *K*+/Na+ ratios in the cytosol for proper functioning. MEL plays a critical function in maintaining ion homeostasis by up-regulating the transporters like NHX1 (vacuolar Na+/*H*+ antiporter gene) (Li et al., 2010). Applying MEL under salt stress conditions can boost the synthesis of ABA, activating various signaling pathways while up-regulating transporter genes such as NHX1, HKT1, and AKT1 (Yu et al., 2018). Because MEL treatment causes increases in SOS1 expression in NaCl-treated roots, this may directly contribute to Na^+ export from roots and retention in stems, thereby preventing $Na^+$from reaching photosynthetic leaf tissues (Li et al., 2017). However, despite numerous studies confirming the effectiveness of exogenous MEL in improving plant salinity tolerance, more research is needed to determine whether or not endogenous MEL is known to be effective in plant salt stress resistance (Julkowska and Testerink, 2015; Chen et al., 2017). Such as MET solutions (10–500 μM) were used to restore the effect of NaCl-decreased seed germination potential, germination index, and vigor index on rice genotypes by reducing Na+ and Cl− contents in roots and leaves and enhancing the activities of antioxidant enzymes (such as catalase and superoxide dismutase) in roots and leaves resulted in a decrease in H2O2 level. Moreover, MET pre-treatment enhanced the transcription of OsSOS1 in roots and of OsCLC1 and OsCLC2 in roots and leaves. The results provide a basis for the chemical regulation of salt tolerance (Li et al., 2017). Further, appropriate melatonin (100 μmol/L) treatment reduced the effects of NaCl stress caused the net photosynthetic rate, stomatal conductance, maximum photochemical efficiency, PSII effective photon yield, photochemical quenching, and other indicators of seedlings (Hu et al., 2022). Overall, MEL modulates transporter protein expression and induces anti-oxidant enzyme levels to mitigate salt stress.

Heavy metal stress causes damage to the chloroplast's ultrastructure and membrane potential, DNA and protein damage, enzymatic inhibition, and the inhibition of chlorophyll *b*iosynthesis by interfering with nutrient uptake and production (Singh et al., 2016). In addition, it raises the level of ethylene in the atmosphere, slows the growth of shoots and roots, decreases CO2 fixation, and restricts sugar transport. Heavy metals stimulate the production of ROS in plants from PSI and PSII, resulting in formalized oxidative stress. This toxicity of heavy metals could be mitigated by the exogenous application of MEL (Hoque et al., 2021)

UV-B (280–315 nm) severely damages plant growth and development by disrupting the integrity and function of essential macromolecules (DNA, lipids, and proteins), causing oxidative damage and reducing photosynthetic capacity (Zhang et al., 2012). Alpine and Mediterranean plants, which receive more UV exposure than their counterparts at lower latitudes, have higher MEL levels. It has been shown that in spinach leaves with fluorescent ROS probes, high doses of UV-B cause an overabundance of ROS production, particularly of $O_2^-$and O_2^-in plant cells via proteins involved in light reactions and the Calvin-Benson-Bassham (CBB) cycle, which is similar to other abiotic stresses (Yao et al., 2021). Alternating electron sinks relax mitochondrial or chloroplastic electron flow because TBARS (Thiobarbituric acid reactive substance) levels continuously decrease over time, with exogenous MEL treatment improving the photochemical efficiency of PSII (Fv/Fm) (Iqbal et al., 2021). This application was also linked to increased antioxidant enzyme activity and expression in leaves exposed to UV-B (APX, CAT, and POD) and a more significant drop in the H_2O_2 level (Yao et al., 2021). With the application of MEL, the inhibitory effects of UV-B radiation on photosynthetic parameters, chlorophyll fluorescence parameters, stomatal apertures, chlorophyll levels, and leaf membrane damages were all significantly reduced or eliminated and can be used for stress protection.

2.2. Role in biotic stress

MEL is considered an eco-friendly molecule that induces the protection of plants against biotic stress. Various studies classify the role of melatonin as an antioxidant, immunomodulatory, and neuroprotective, and that displays anti-inflammatory activities in animals. Hence, it can be utilized as beneficial medicine to suppress diseases. However, recent studies show its role in plant-pathogen interaction has shown significance in plants. Further details have been discussed extensively in the later section (Table 2).

2.2.1. MEL as an antiviral and antibacterial agent

Studies on viruses have demonstrated the antiviral effectiveness of MEL in plant species. For example, exposure to 100 μm of MEL in tomato seedlings has helped reduce tobacco mosaic virus infection by activating the NO-dependent pathway that increased salicylic acid concentrations (Zhao et al., 2019). Another study supports that MEL production eradicated apple stem groove infection from a gala variety of apples and produced virus-free plants (Chen et al., 2019). In the case of animals, a study showed that applying MEL has resulted in fewer harmful effects caused by the spread of the encephalomyelitis virus. Further, the study depicted more occasional blood and brain viruses that control infection in mice (Wongchitrat et al., 2021). Also, the bioactivity of MEL has been tested for its defensive properties in both in vivo and in vitro conditions. Various studies have shown its bactericidal activity in gram-negative and positive bacteria, along with methicillin-resistant *S. aureus* and *A. baunmanni.* These studies also reveal the mechanisms underlying biotic stress, such as regulating cellular cAMP and Ca2+ and cytoderm destabilization on binding to the cell wall (Masadeh et al., 2017; Norbury et al., 2016, Ma et al., 2020).

Moreover, MEL was effective against phytobacterial pathogens due to its antibacterial activity. For instance, applying exogenous

Table 2
Role of melatonin in biotic stress tolerance of different crops.

Pathogen	Crops	Pathogen	Delivery method and melatonin dosage (μM)	Molecular mechanism	Refs.
Plant-Virus	Tobacco and tomato	Tobacco mosaic virus	Root irrigation, 100	Upregulation of PR1 and PR5 genes by increased prodcution of salicylic acid (SA)	Zhao et al. (2019)
	Apple	Apple stem grooving virus	Shoot proliferation medium, 15	Crosstalk of melatonin with phytohormones like SA, jasmonic acid and auxin further activates plant defense genes	Chen et al., (2019)
	Rice	Rice stripe virus	Leaf treatment, 10	Provides resistance from infection through a nitric oxide (NO) dependent pathway	Lu et al. (2019)
Plant-bacterial	Benthi	Pseudomonas syringae	Leaf treatment, 1 or 10	Expression of defense genes PR1, PR5, and PDF1.2	Zeng et al. (2022)
	Arabidposis	Pseudomonas syringae	Leaf treatment, 10	Pathogenesis-related (PR) genes by the harmonizing signaling between SA and ET	Nehela and Killiny (2020)
	Arabidposis	Pseudomonas syringae	Leaf treatment, 10		Lee et al. (2015)
	Valencia orange	Candidatus Liberibacter asiaticus	Leaf treatment, upto 500	melatonin and SA biosynthesis pathways share a common precursor, which is generated from shikimic acid, and both play a relevant role in citrus physiology	Wei et al. (2017)
	Arabidposis	Pseudomonas syringae	Plant culture medium, 50	Activities of CWI and vacuolar invertase (VI)	Zhao et al. (2015)
	Manihot esculenta	Xanthomonas axonopodis pv. manihotis	Leaf treatment,200	MeRAV1 and MeRAV2 Tf's are responsible for plant disease resistance against cassava bacterial blight.	Wei et al. (2018)
	Arabidposis	Pseudomonas syringae	Leaf treatment, 1	Activation of PR1 and ICS1 expression genes via MAPK signaling in coexistence H2O2 and NO	Lee et al. (2017)
Plant-fungal	Plumleaf crab apple	Diplocarpon mali	Root irrigation, 50−500	Maintain intracellular H2O2 concentrations	Yin et al. (2013)
	Lupin	Penicillium spp.	Seed treatment, 20−70	Increased NO and melatonin levels through ROS	MB and J (2018)
	Strawberry	Botrytis cinerea and Rhizopus stolonifer	Fruit dipping,100	Increase in Antioxidant enzyme activities, in stored strawberry fruits	Aghdam et al. (2017)
	Watermelon	Podosphaera xanthii and Phythophthora capsici	Leaf treatment,100	Increased expression of PTI- and ETI-associated genes conferring resistance against the disease	Mandal et al. (2018)

melatonin on rice leaves reduced the occurrence of bacterial leaf steak caused by *Xanthomonas oryzae* by 17% (Pal et al., 2021). Additionally, MEL treatment activates transcriptional factors viz. MeRAV2 and MeRAV1 confer disease resistance against cassava's bacterial blight (Wei et al., 2018). During biotic stress, activation of defense pathways is regulated by differentially expressed genes of the Pathogenesis-related (PR) family and plant defensins, followed by upregulation of genes involved in mitogen-activated protein kinase, signal transduction, and salicylic acid (SA) pathway (Verma et al., 2016). This triggers the plants' classical Pathogen associated molecular patterns (PAMP)-triggered immunity (PTI) and Effector-triggered immunity (ETI) responses (Pandey et al., 2018). Moreover, against bacterial strain DC3000 (Pst) on treatment with MEL results in cell wall strengthening and activation of SA- and NO-dependent pathways in Arabidopsis (Zhao et al., 2015). A similar study reported the induction of pathways in the presence of sugar and glycerol along with MEL exposure. Even in studies related to transcriptome data, ETI and PTI genes were observed in watermelon when MEL was exogenously applied (Weeda et al., 2014; Mandal et al., 2018). MEL-induced stomatal closure plays a prominent role in preventing the invasion of bacteria Pseudomonas syringe pv. tomato (Pst) DC3000 via activation of mitogen-activated protein kinase (MAPK) and NADPH oxidase-mediated reactive oxygen species production (Yang et al., 2021). Similar studies of MEL-induced plant biotic stress defense has been highlighted in Table 2.

2.2.2. *Role of MEL in the plant-fungal pathosystem*

Fungal diseases have caused tremendous crop yield and production loss over the years. Host-fungus interactions in plants trigger the defense mechanism with hormonal growth fluctuations, which could be used to control the fungus. For example, in the late blight of potatoes, an elevated level of MEL leads to fungicidal susceptibility, increases the vulnerability of *Phytophthora infestans*, and promotes fungicide treatment efficiency. Another study reported tomato resistance against the disease caused by the pathogen *Botrytis cinerea*, which activated the jasmonic acid signaling pathway as a defense response (Zhang et al., 2017). Foliar pathogens like powdery mildew and soil-borne oomycetes in cucurbits and watermelons, differential expression of genes related to ETI and PTI was observed (Mandal et al., 2018). Applying 100 μM, MEL-activated genes related to antioxidant enzymes reduced the powdery mildew of cucumber and decreased the disease index (Sun et al., 2019). However, studies on the synergistic effect of MEL with ethylicin (an oomycete antifungal) showed a positive impact by inhibiting the *Phytophthora nicotianae* via amino acid metabolic homeostasis (Li et al., 2018). Along with the above interventions, a similar study describes the defensive function of MEL against disease-causing fungi in plants and green mold disease caused by *Penicillium digitatum* reacting by scavenging ROS in diseased fruits (Lin et al., 2019). Various MEL defense mechanisms concerning viruses, bacteria, and fungi are summarized in Table 2. They further indicate that using MEL as a stress protectant for commercial field applications needs further exploration.

3. MEL-mediated plant physiological and biochemical changes under stress

It's well accepted that abiotic stressors are severe and causes significant obstacles to increasing crop output. Depending on how severe and prolonged the stress is, numerous physiological and metabolic processes vary, eventually affecting crop output under salinity stress (Rahman et al., 2016). Even though irrigated land accounts for only 15% of the total cultivated area, it generates one-third of the world's food due to its higher productivity than rainfed land (Munns and Tester, 2008). Applying MEL protects stress-induced physiological and biochemical changes to mitigate the adverse effects on the plant. This section describes essential processes involved in MEL-mediated plant protection.

3.1. Photosynthesis and photoprotection

In response to salt stress, MEL enhances photosynthetic activities. It protects cells from injury caused by higher ROS concentrations in cells by promoting recovery of the electron transport chain during photosynthesis, protein synthesis in D1, and photochemistry efficiency (Fv/Fm) of photosystem II (PSII) (Zhou et al., 2016) and photochemical quenching (qP) (Zhou et al., 2016; Hao et al., 2017). It also has antioxidant properties that protect chlorophyll and accessory pigments (Tal et al., 2011; Lazar et al., 2013; Shi et al., 2015).

3.2. MEL as the safeguard of chloroplast ultrastructure

Three processes are directly hindered by abiotic stresses, specifically drought: (a) supply of CO_2 to photosynthetic sites, (b) photochemical reactions connected with light energy use (c) chemical reactions associated with CO_2 reduction. These changes result in reduced photosynthesis under low soil moisture conditions. Biochemically photosynthetic pigments are depleted due to changes in chlorophyll photo-oxidation, destruction of chloroplast structure and the photosynthetic machinery, and suppression of Chlorophyll biosynthesis (Wang et al., 2013a). Under water-deprived conditions, a significant increase in chlorophyll content and stress-related phytohormones was linked to endogenous MEL levels. While growing in extreme heat and dryness, MEL is produced endogenously in mitochondria and chloroplasts by increasing the grana lamella's compactness and improving the leaf's relative water content (Tan et al., 2013). It aids in maintaining cell turgor by increasing stomatal opening and conductance capacity and recovery in the form of palisade tissue by lengthening stomata (Antoniou et al., 2017; Dai et al., 2020). Minimizing non-photochemical energy dissipation enhances the electron transport system, particularly photosystem II (Fleta-Soriano et al., 2017). Further, increasing PSII yield (Fv/Fm) and the effective quantum yield of PSII [Y(II)], the non-photochemical quenching (NPQ) and photochemical quenching (qP) were significantly reduced, which have a protective effect in plants under water deficiency situations (Ding et al., 2018; Sharma and Zheng, 2019; Karaca and Cekic, 2019; Huang et al., 2019). Similar studies have been carried out on cucumber (Zhang et al., 2013), kiwifruit (Liang et al., 2019), apple (Wang et al., 2016), plum leaf apple (Li et al., 2015), grapes (Meng et al., 2014) and tomato to show the effect of MEL application on reducing drought-induced photosynthetic machinery damage (Liu et al., 2015). During drought stress, MEL restores chlorophyll content by reducing enzyme activity of chlorophyllase (Chlase), pheophytinase (PPH), and chlorophyll degrading peroxidase and enhances photosynthetic, transpirational, and stomatal conductance (Liang et al., 2018; Karaca and Cekic, 2019). Chlorophyll metabolism also involves the enzyme pheophorbide-a-oxygenase (PAO). MEL reduces the transcript level of the PAO enzyme, which delays leaf senescence in the presence of water stress. Exogenous MEL increases Calvin cycle enzyme regulation under drought stress (Sadak et al., 2020). It is known that MEL increases the transcript levels of several key carbon fixation pathway enzymes, including RUBISCO, PGK, GAPA, and FBA (Liang et al., 2019; Sharma et al., 2019). All these reports indicate the crucial role of MEL in protecting the photosynthetic machinery under stress conditions which could potentially be explored for safeguarding the crop yield in stressful environments.

4. MEL-induced signaling pathways to provide stress tolerance

4.1. ROS-related pathways

Environmental stress, such as high salinity and drought conditions, generates ROS and damages membranes, lipids, and DNA. This results in the activation of signaling cascades, which activate signaling pathways that induce highly expressed genes that remove reactive oxygen species. ROS molecules degrade the PSII assembly, resulting in an imbalance in photosynthetic redox signaling and the suppression of PSII repair, both detrimental to the plant (Mishra et al., 2023). Both endogenously produced and exogenously given MEL has been shown to prevent oxidative injury caused by ROS significantly. MEL works by increasing the scavenging activity of the antioxidant enzymes SOD, POD, and CAT, which helps to protect cell membranes from damage (Rodriguez et al., 2004). MEL can also improve the efficiency of the mitochondrial electron transport chain, lowering electron leakage and forming free radicals, protecting antioxidant enzymes from oxidative damage, and acting as a natural sleep aid (Parida and Das, 2005). Melatonin therapy increases the activity of POD and APX under salt stress, lowering the percentage of electrolyte leakage and the amount of MDA and reducing oxidative damage. There could be two possible explanations for this response: (i) direct free radical scavenging and (ii) an increase in the antioxidant enzyme activity (Li et al., 2012). The findings of this study suggest that MEL reduces the porous nature of plasma membranes and lipid peroxidation in membranes and helps maintain the integrity and functions of the maize membrane against salinity, thereby alleviating salt toxicity and improving crop growth.

Drought stress is responsible for generating higher concentration ROS molecules examples include singlet oxygen and superoxide anions. Because of the peroxidation of the thylakoid membrane, ROS were generated in photosystem I (PSI) and disrupted PSII, resulting in the denaturation of the two photosystems (Oladosu et al., 2019). As a result of electron leakage from ETC complexes I (NADH/ubiquinone oxidoreductase) and IV, mitochondria considerably produce ROS (reactive oxygen species) and RNS (reactive nitrogen species) during drought, impairing mitochondrial respiration (Turk and Genisel, 2020). ROS and RNS are created during mitochondrial respiration, which causes oxidative stress in abiotic stresses. MEL has been shown to increase ROS scavenging efficiency and activate plants' antioxidative defense mechanism to protect them. One such mechanism is an increased ascorbate-glutathione cycle enzyme to scavenge H_2O_2 (Li et al., 2015; Liu et al., 2015b; Meng et al., 2014). Plants' ability to cope with drought-induced stress is facilitated by an enzyme system known as the AsA–GSH pathway, also known as the Halliwell–Asada pathway (Sharma et al., 2019). To tolerate drought-induced oxidative stress, plants must have high AsA/(AsA + DHA) and GSH/(GSH + GSSG) ratios. The four enzymes dehydroascorbate reductase, ascorbate peroxidase, monodehydroascorbate reductase, and glutathione reductase (GR) are critical for plant anti-oxidant response (Bidabadi et al., 2020; Kaya and Doganlar 2019). Endogenous MEL induces the antioxidant response by activating ROS-related pathways to cope with the adverse effect of abiotic stresses and could be applied exogenously for broader crop protection.

4.2. Enhancing reactive oxygen species scavenging enzymes and non-enzyme activity

Plants that received MEL pre-treatment had a lower concentration of H2O2 and O2- and higher levels of the ROS-scavenging enzymes superoxide dismutase, catalase, ascorbate oxidase, glutathione peroxidase, and glutathione reductase (GR). Ascorbate oxidase and dehydroascorbate reductase (Li et al., 2015; 2018; Liu et al., 2015; Meng et al., 2014; Alharby et al., 2020, Bidabadi et al., 2020, Sadak et al., 2020, Dai et al., 2020). The drought adaptive mechanism in plants under water scarcity is actively facilitated by proline, the most crucial non-enzymatic antioxidant, and exogenous MEL administration stimulates proline production. It lowers oxidative stress induction (Meng et al., 2014a, Antoniou et al., 2017), proline synthesis (Wang et al., 2019), and total soluble proteins and sugars (Arnao and Hernández-Ruiz, 2015), and reduces ROS accumulation (Arnao and Hernández-Ruiz, 2020). These are all facilitated by MEL, which aids in drought adaptations through cell membrane stabilization and reduced ROS accumulation. Chemical reactions such as hydrogen donation, addition reaction, substitution, and nitrosation are all part of ROS scavenging of MEL. Structural analysis shows that MEL's anti-oxidant activity is driven by its indole heterocycle (Shirinzadeh et al., 2010). The NH group donates hydrogen ions and side chains (the N-acetyl and methoxy groups), contributing to its enhanced antioxidant properties. Aside from that, MEL application raised heavy metal-polluted seedling concentrations of proline, glutathione, ascorbate, tocopherol, and total polyphenols (Shi et al., 2015; Wang et al., 2013). Overall, this suggests ROS-scavenging enzyme production after MEL application reduces the detrimental effect of abiotic stresses on the crop.

4.3. Cross-talk with signaling molecules and phytohormones/emerging phytohormones

MEL is similar to auxin for root development, shoot growth, seed metabolic function, rhizogenesis, etc., in plants like rice, mustard, sunflower, soybean, cucumber, tomato, wheat, and corn plants (Arnao and Hernández-Ruiz, 2015). Along with structural similarity with auxin, MEL also involves tryptophan as a common precursor for its biosynthesis. Auxins and MEL could co-participate in the different physiological processes involved in plant growth and development, and both hormones also expose some antioxidant properties. Recent research revealed that auxin and MEL are related to enhancing plant root development (Ren et al., 2019). A higher amount of MEL tremendously diminishes root meristem size, while a low amount of MEL helps augment the endogenous concentration of IAA in mustard and Arabidopsis (Chen et al., 2009). Until now, few genes have been discovered to understand the mechanism of MEL in plant systems, and more research is needed to pinpoint MEL biosynthesis and signaling. MEL also shows some distinct relation with Gibberellins because MEL helps boost growth under different physiological processes. Other reports examine the plausible crosstalk with GA. For example, Zhang et al. (2015) evaluated GA4 and MEL crosstalk in cucumbers under salinity stress and found increased expression of the genes that control the biosynthesis of GA. In-depth studies are needed to understand the regulatory roles of MEL and GA in plants. As MEL integrates with ABA during several biological pathways, it can have interactions during plant growth and development with CK. Research revealed that MEL treatment tremendously upregulated the transcripts of CK biosynthesis and factors that trigger signaling TFs (Zhang et al., 2017). MEL's relation with CKs is related indirectly to ABA. In CKs signaling pathway, ARR genes act as downstream transcriptional regulators (Hwang et al., 2001). These ARRs control the network between CK and ABA. Also, the combined application of MEL and CK reduces dark-induced chlorophyll decrease in barley leaves.

MEL reduced ABA's production to promote stomata function under drought stress and performed a direct involvement in hormonal cross-talk (Sharma and Zheng, 2019). They also discovered that MEL resulted in thicker epidermal cells, undamaged chloroplast grana lamellae, and increased leaf photosynthetic activity. MEL administration increased the expression of ABA degradation genes (MdCYP707A1 and MDCYP707A1) and decreased the expression of the biosynthetic ABA pathway gene under drought stress (9-cis-epoxy carotenoid dioxygenase 3, NCED3) (Li et al., 2021). Stomatal regulation occurs when ABA concentration and antioxidant molecules are balanced synergistically under stressful conditions (Li et al., 2016; Prakash et al., 2019; Sharma and Zheng, 2019).

MEL also increases nitric oxide synthase activity while decreasing the expression of S-nitroso glutathione reductase, which helps NO build up more quickly (Zhu et al., 2019). NO's principal role in plant cells is to control the cellular redox balance. Under external stimuli and developmental signals, NO can scavenge free radicals and minimize oxidative damage without relying on receptors. On the other hand, the nitrate reductase protein has been identified to catalyze NO generation from nitrite (NR) (Alamri et al., 2022). Using MEL and NO therapy, damage from alkaline stress was reduced by decreasing Na^+ accumulation, activated gene expression in the defense response signal pathway, and improved K^+ absorption, antioxidant enzyme activity, and the ability of ASA−GSH to detoxify (Liu et al., 2015b; Zhao et al., 2018). Phytohormones' interaction with MEL could govern the stress protection induced through different growth and developmental pathways.

4.4. Upregulating calcium signaling

To activate calcium signaling in response to MEL, calcium-binding proteins like CaM, CaM-like proteins, and Calcineurin B-like proteins (CBLs), as well as $Ca2^+$-dependent protein kinases (CDPKs), are synthesized. These proteins bind to Ca^{2+} and activate various downstream signaling pathways Ca^{2+} signaling increases antioxidant enzyme activity like ascorbate peroxide, glutathione reductase, and superoxide dismutase (Ahamad et al., 2015). Exogenous application of MEL resulted in increased plant superoxide dismutase, ascorbate peroxidase, and peroxidase activity (Li et al., 2012; Zhang et al., 2014; Jiang et al., 2016).

4.5. Glutathione swimming pool activity

The glutathione ascorbate cycle is well-known for its defensive role in plants' ability to cope with stress (Zhang et al., 2015). The glutathione pool activity regulates hydrogen peroxide levels, which is critical for reducing plant stress (Turk and Genisel, 2020). While GSH is oxidized by reactive oxygen species (ROS) and protects sensitive cellular components from oxidation, it is also a primary nonprotein source linked to the antioxidant barrier. The ratio of reduced GSH to oxidized GSSG changes during H_2O_2 degradation can be used to determine cellular redox balance (Espinosa-Diez et al., 2015). Phytochelatins, which bind to heavy metals, are synthesized using glutathione as a precursor (Grill et al., 1987). As a result, GSH plays a vital role in heavy metal detoxification and cellular ionic homeostasis maintenance. Tolerance to abiotic stresses may be improved by phytochelatin synthesis and restricted translocation of HMs to foliar parts. Therefore, this pathway could be a mechanism of MEL for plant stress protection.

5. Biotechnological interventions of MEL for future generation climate-smart crop generation

In crop production, the role of MEL becomes vital due to its involvement in the rising of biomass, seed growth, enhancement in fruit ripening, photosynthetic activities, and building tolerance to different kinds of biotic and abiotic stresses (Asif et al., 2020). Therefore, to know the mechanism behind the functioning of MEL under abiotic and biotic conditions (Tiwari et al., 2020), biotechnology can open a new path in the field of stress biology in plants; furthermore, it is also helpful in exploring genetic alterations that occur on the application of MEL in the plant during the unfavorable condition. The molecular and physiological process involved in the adaptation of crop plants under different biotic and abiotic conditions during the application of MEL can be well studied through modern techniques like transcriptomics, metabolomics, and proteomics of specific transcription factors and heat shock proteins (Lal et al., 2021). MEL studies using biotech intervention can serve as an alternative approach to mitigate stress effects on the plant. Hence, the MEL effect can be well studied using modern breeding and biotechnological tool, and information thus generated can be utilized to improve plant response to different stress conditions (Debnath et al., 2019). Another aspect of MEL study, which can be fulfilled through biotechnology and genetic engineering, is to study its crosstalk and interaction with phytohormones, polyamines, and different singling molecules to mitigate the harmful effect of abiotic stress (Arnao and Hernández-Ruiz, 2015). The advanced CRISPR-Cas9 technology can effectively specify the function of MEL, H2S, Ca2+, H_2O_2, NO, and different signaling molecules and MAP kinase-related pathways important for inducing MEL responses against plant stress tolerance (Raza et al., 2022). The recent information on melatonin synthesis in chloroplasts and mitochondria is highly complex and must be considered for CRISPR/cas9 modification in plants (Raza et al., 2022). Melatonin-based genetic engineering could unfold the mechanism behind plants' abiotic and biotic stress tolerance (Nguyen et al., 2018). Furthermore, extensive effort has to be made in the research area to unravel molecular mechanisms involved in plants during stress conditions on the application of melatonin (Sun et al., 2021). The upcoming experimental investigation should consider the primary melatonin synthesis pathway by creating overexpression genes and in-del (insertion-deletion) mutants using CRISPR/Cas9 technology in various crops for the genes essential for synthesizing MEL plants (Razzaq et al., 2021).

6. Future perspective

MEL is an emerging stress protectant also synthesized by the plant endogenously. MEL biosynthesis and catabolism reaction are crucial in plants coping with various abiotic stresses. Organelles like mitochondria and chloroplasts are involved in the biosynthesis of MEL. Recent research revealed that some enzymes are involved in the biosynthesis of MEL in cytoplasm and ER. It is a pleiotropic molecule and possesses some amphiphilic properties. MEL may present in different parts of the plant anatomy, and by scavenging RNS and ROS, it plays a crucial role in mitigating various abiotic and biotic stresses directly. By improving the photosynthetic system, recovering leaf ultrastructure, activating antioxidants in plants, and stimulating plant growth regulators, MEL indirectly helps the plant to overcome stress conditions. Research has revealed some significant progress, and future studies should focus on exploring MEL metabolism by genetic tractability of reference systems and various available molecular tools. The status of melatonin has been changed from scavenging ROS to a multi-regulatory molecule that involves stimulating some indispensable physiological processes in plants under unfavorable environments. It is an essential component that regulates redox homeostasis. Thus, it can be a stimulator to enhance fortified plants' improved photosynthesis. Trials should be conducted at the field level to examine the exogenous application of MEL. The pathways mediated by MEL have no accurate clarification, and this issue should be addressed. Future studies should be focussed on MEL functions with various plant hormones during different physiological processes. Several isomers were identified in plants that should be more engaged for better understanding. The evidence suggested the MEL upregulates ETI and PTI defense-related genes. Plant growth promotion rhizobacteria (PGPR) have been extensively studied due to their beneficial role in shielding plants against pathogenic diseases. Many studies have reported that PGPR can produce melatonin and subsequently raise its endogenous levels in different plant organs. However, it is necessary to investigate in detail the effect of combined applications of melatonin and PGPR on plant defense against several environmental stressors. Also, its synergistic effect with antifungal, antibacterial, and antiviral treatments. Further, the interactions between melatonin and other phytohormones and their role in transcriptomic and proteomic modifications in plants regarding abiotic stress signaling responses need to be explored. We also suggest that there is a need to identify melatonin receptors and MT-mediated signaling pathways.

Declaration of Competing Interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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