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Recent Progress on Melatonin-Induced Salinity Tolerance in Plants: An Overview

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ABSTRACT

In this context, it is necessary to select and develop salt-tolerant genotypes that can grow in salty soils and have high yields, and formulate strategies which may enhance the plant survival under salinity stress. Melatonin (N-acetyl-5-methoxytryptamine) is an important biological hormone that provides resistance to abiotic stress conditions and can be secreted by plants. Melatonin concentration in plants varies depending on genotype, temperature and growth period. Increase in melatonin concentration is associated with increased SNAT and HIOMAT/ASMT enzyme activity. It plays an important role in gibberellic acid and abscisic acid biosynthesis during the germination and provides plant growth and development. Exogenous application of melatonin significantly alleviates chlorophyll degradation and stomatal closure caused by salt stress, improves photosynthesis and enhances plants' salt tolerance. Besides it significantly reduces the harmful effects of salinity by regulating plant physiology, improving plant morphology, photosynthesis and activities of antioxidant enzymes. The present review discusses the recent studies on the effect of melatonin on plant growth and physiology against salt stress that have important impacts on plant growth and development have been given according to the findings of various researches. It also highlights the mechanim/s of melatonin-induced salinity stress tolerance in plants.

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Introduction

Salinity is one of the most significant abiotic stresses that hinders growth and development and causes important yield losses especially in arid and semi-arid areas. Every year, 2 million hectares of the world's agricultural land (about 1%) suffer from salinity, resulting in huge yield losses. High salt degree causes ion toxicity, hyperosmotic stress, as well as secondary stresses such as oxidative damage and leaf senescence (Ke et al., 2018). Salinity negatively influences plant physiology through more than one mechanism. First, the accumulation of sodium ions damages cellular organelles, inhibits protein synthesis and enzyme activities, and hinders photosynthesis and respiration. Second, salt stress reduces nutrient intake and/or transport to shoots, causing in a nutrient imbalance. Third, it disturbs osmotic balance in the soil and causes a physiological drought in the plant by preventing water intake of the roots (Li et al., 2017).

Salt stress causes ROS accumulation that triggers K^+ flow through non-selective cation channels. It has been observed that with exogenous application of melatonin, K^+ influx from stem cells and mesophyll tissues of sweet potato is significantly reduced (Yu et al., 2018).

Salinity stress affects the yield and quality of the plant negatively by changing the soil structure (Hancı, 2019). Ionic toxicity caused by Na^+ accumulation especially at high doses causes deterioration in biochemical reactions and prevents seed germination. The reduction of photosynthetic activity, the accumulation of organic acids and osmolites, changes in carbohydrate metabolism are the physiological and biochemical responses of plants to salinity stress (Dawood and El-Awadi, 2015). Photosynthesis, one of the important physico-chemical processes, is responsible for energy in higher plants and is highly susceptible to salinity. During stress, the intercellular CO_2 content in the leaves decreases due to the closure of the stomata. In addition, salinity reduces NADPH consumption by the Calvin Cycle, restricts chlorophyll synthesis and Rubisco activity, and disrupts photosynthetic electron transport. Salinity-induced inhibition of photosynthetic electron transport leads to excessive accumulation of toxic reactive oxygen species (ROS) and disruption of cellular redox homeostasis. The excess accumulation of ROS encourages DNA mutation (Ke et al., 2018), chlorophyll and protein degradation which ultimately reduce the yield of plants (Liang et al., 2015, Ahmad et al., 2020) and decrease photochemical efficiency of photosystem II (PSII). Higher production of ROS damages membranes, breaks the DNA chain, and inactivates various vital enzymes through lipid peroxidation (Li et al., 2017). Melatonin (MEL), a small molecular weight and tryptophan derivative indolamine molecule found in all kingdoms, from prokaryotes to eukaryotes, animals to plants (Kabiri et al., 2018; Varghese et al., 2019; Xu et al., 2019; Wang et al., 2021) as well as a free radical scavenger and broad-spectrum antioxidant, and plays a role in various biological processes in plants (Dawood and El-Awadi, 2015; Ke et al., 2018). In the past studies, it has given information about melatonin formation and exogenous application of melatonin in plants exposed to abiotic stress. In this review, recent developments in exogenous melatonin-induced salt tolerance and morphological, physiological and biochemical responses of plants were evaluated.

Overview on Melatonin

Melatonin is found in the roots, stems, leaves, fruits, flowers and seeds of plants in more than twenty dicotyledonous and monocotyledon plant families (Kul et al., 2019; Siddiqui et al., 2019; Khan et al., 2020). It plays an important role in regulating plant growth and development, such as chlorophyll synthesis, photosynthesis, callus formation, flowering, root formation and senescence of leaves (Dawwod and El-Awadi, 2015; Zhan et al., 2019). Melatonin was first described in the animal pineal gland. Today, it is known to be synthesized by various plants (Wang et al., 2021). Melatonin is synthesized in mitochondria and chloroplasts in plants (Siddiqui et al., 2019). It was observed that the melatonin content increased during the maturation period in some plants (Van Tassel et al., 2001). The amount of melatonin found in plants varies according to species, genotype or varieties within the same species, and even different growth periods of individuals of the same genotype. Although the melatonin content in green tomato fruits is low, it has been found in high amounts in ripe and red coloured fruits. The melatonin level, which was high in the young plant leaves and roots, decreased as the pepper plants matured. Melatonin increased significantly in fruits and seeds with the ripening of the fruits (Yakupoglu et al., 2018). A similar situation was observed in the eggplant plant and it was emphasized that the melatonin contained in the roots was sent to the reproductive organs such as flowers and fruits to protect against oxidative stress (Korkmaz et al., 2017). The highest melatonin content in plants is in generative organs such as fruit, seeds and flowers. The reason for this is thought to be due to the fact that melatonin content functions in the antioxidant defence mechanism, especially in buds and dried seeds (Yakupoglu et al., 2018).

Melatonin acts as a free radical scavenger and an antioxidant. A single melatonin molecule can scavenge 10 reactive oxygen species (ROS) / reactive nitrogen species (RNS) unlike other antioxidants. It also interacts with ROS by improving antioxidant (AsA-GSH) concentrations (Korkmaz et al., 2017; Hacısevki and Baba, 2018; Khan et al., 2020).

Low dose melatonin (0.1 mM) stimulated root growth in *Brassica juncea* while high dose (100 mM) application inhibited growth (Chen et al., 2009). Melatonin reactions varied according to plant species. For example, the response of lupine to melatonin application appeared after 24 hours, while reactions were observed after 72 hours in barley plants. Roots are organs that are directly affected under stress conditions and are highly sensitive to changes in pH, salinity, the presence of oxygen, toxic elements and water potential around the root. But a strong root system is effective in resisting the negative effects of stress. Melatonin application had a significant effect on ethylated hypocotyls and roots of *Lupine albus* and *Brassica juncea* plants. Melatonin caused the emergence of root primordial from pericycle cells, altered distribution and formation time of adventitious or lateral roots (Arnao and Hernandez-Ruiz (2007) and a changed in the number and length of adventitious and lateral roots. In high salt conditions a significant decrease in plant growth, net photosynthesis rates and chlorophyll contents was observed. Melatonin application has reversed and alleviated these negative conditions. Thus, the plants have a stronger root system and their photosynthetic activities have increased. In addition, melatonin helped the plant cope with stress conditions by maintaining membrane integrity (Zhang et al., 2015; Khan et al., 2020).

Exogenous Application of Melatonin at Germination Stage Under Salinity Stress

Melatonin increased the germination rate and germination index slightly in cool climate vegetables under 300 mM NaCl stress conditions (Hancı, 2019). Similarly, Tan et al. (2012). emphasized that high MEL content in plants increases the germination rate of seeds in salinity adverse conditions and improves quality. For stevia seeds, 5 µM nelatonin was the best concentration for seed germination, while 20 µM had a positive effect on the biomass of the plants. Salt significantly reduced seed germination, but application of MEL at 50 mM NaCl alleviated this effect. The highest stevioside and rebaudioside A (Reb A) values were obtained from 5 and 20 µM MEL application of seeds, respectively. Steviol glycoside gene expression in young leaves varied according to MEL concentration (Simlat et al., 2020).

Salt stress caused electrolyte leakage (EL) as well as accumulation of hydrogen peroxide (H_2O_2), malondialdehyde (MDA), organic (proline, soluble sugars) and inorganic (Na^+, Cl^-) osmotic substances. In addition, K^+ content and K^+/Na^+ ratio decreased which prevented melatonin synthesis by salt stress and significantly affected seed germination by disrupting cell membranes. Melatonin application under salt stress conditions reduced the negative effects of salt on cotton seeds and also reduced EL, H_2O_2, MDA, Na^+ and Cl^- contents. However, it also promoted melatonin, soluble sugar, soluble protein, proline and K^+/ Na^+ contents. To protect cotton seeds from salt stress, application of 20 µM melatonin promoted germination of cotton seed and increased tolerance to salt stress (Chen et al., 2020).

The melatonin content in the roots and leaves of the grapevine raised importantly with the salinity, which increased with the intensity of the stress (Yandi, 2018). In high salinity conditions, germination and root elongation were inhibited, plant growth, net photosynthesis rate, chlorophyll content decreased. Exogenous melatonin application positively affected growth by maintaining intact roots and photosynthetic capacity (Zhan et al., 2019).

In salt stress conditions, the regulatory role of melatonin and the MsPMTR1 gene were observed to be effective in germination with the application of melatonin to alfalfa seed (Yu et al., 2021). Melatonin application promoted germination in cucumber by regulating the interaction of antioxidant systems, abscisic acid (ABA) and gibberellin (GA4) under high salt stress conditions (Zhang et al., 2014). Similar results, Zhang et al. (2017b) was also found in another study. Chen et al. (2020) observed that melatonin application to cotton under salt stress provides seed germination and osmotic regulation. Melatonin application to turfgrass under stress conditions caused more amino acid, organic acid and free sugar accumulation, providing tolerance to salt stress (Shi et al., 2015a).

Effect of Morphological, Physiological and Biochemical Parameters

Melatonin had beneficial effects on the growth of tomato seedlings under both salinity and control conditions. The exogenous application of melatonin increased the physiological and biochemical parameters (Chlorophyll a (Chl a) and Chlorophyll b (Chl b), carbonic anhydrase (CA), Rubisco, proline, pyrroline-5-carboxylate synthase (P5CS) and total soluble carbohydrates (TSC) of tomato seedlings under normal conditions not only significantly increasing plant growth but also resulting in a better tolerance to NaCl stress of tomato seedlings. The role of melatonin in salt tolerance is associated with photosynthesis, antioxidant, proline and carbohydrate metabolism and the regulation of enzymes involved in the ASC (ascorbate) – GSH (reduced glutathione) cycle. It was also emphasized that melatonin may be responsible for maintaining high GSH / GSSG (oxidized glutathione) and ASC / DHA (dehydroascorbate) ratios (Kul et al., 2019). Li et al. (2012) stated that melatonin application in *Malus hupehensis* Rehd under high salt stress conditions significantly improved plant growth and photosynthetic capacity. Melatonin application to broad bean plants under salinity stress improved growth parameters such as plant height, leaf number, plant fresh and dry weight, relative moisture content, chlorophyll a, b and carotenoid values, phenolic compounds, indole acetic acid, total carbohydrate content, K^+, Ca^{2+}, as well as K^+ / Na^+ and Ca^{2+} / Na^+ ratios (Dawood and El-Awadi, 2015). Similarly, chlorophyll content was found to be higher in plants treated with melatonin in saline conditions in other studies (Chen et al., 2018; Mohamadi and Karimi, 2020; Jiang et al., 2021; Park et al., 2021).

The application of 50 μM melatonin to tobacco plants under salt stress conditions increased the enzyme activities with pigment, proline and malondialdehyde contents. Therefore, the application of melatonin to the leaves in tobacco reduced the negative influences of salinity by regulating stress responses (Kaya and Inan, 2018). Exogenous application of MEL against salt stress in pepper seedlings increased the tolerance to stress. In plants exposed to stress, 5 μM MEL application gave the best results in terms of stomatal conductivity, plant height, wet weight, electrical conductivity values, while 10 μM MEL was found to be the best in terms of MEL amount, chlorophyll content, total phenolic and carotenoid content. The study results highlighted that MEL can be used as a plant growth regulator to increase plant salt tolerance and application of 5 μM MEL to pepper seedlings against salt stress can be recommended to reduce stress tolerance and prevent damage (Yakupoglu, 2020).

Melatonin application in oats under salt stress conditions significantly affected various morphological, physiological and biochemical parameters. In addition, melatonin caused changes in the expression of genes encoding core PSII proteins. Melatonin increased PSII activity under salt stress by suppressing stress-induced PSII damage and promoting ROS scavenging by enzymatic antioxidants (Varghese et al., 2019).

Melatonin reduced oxidative damage under salt stress conditions by directly scavenging H_2O_2 or increasing the activity of antioxidant enzymes and antioxidant concentrations. Therefore, plants treated with melatonin effectively increased their salinity tolerance. Similarly, Jiang et al. (2016a) emphasized that MEL application to maize plants under salt stress caused a significant improvement in growth, photosynthetic capacity, antioxidant enzyme activity and homeostasis.

Melatonin (100 μM) application reduced the effects of NaCl stress in *Rosmarinus officinalis* L. (Mohamadi and Karimi, 2020). The most protective effect against 150 mM salt stress was observed at 100 μmol/L MT. MEL significantly decreased the inhibitory effects of salinity on root and shoot growth, chlorophyll and ion leakage, while increasing the content of antioxidant enzymes, proline content, intracellular polyamine and melatonin. It also led to an increase in nutrient content. Therefore, exogenous melatonin application alleviated salt damage by increasing antioxidant enzymes, osmotic activity adjustment, food intake, and polyamine biosynthesis (Kamiab, 2020). Various studies have shown that one of the roles of melatonin under salinity conditions is promoting growth by increasing leaf area, root fresh and dry weight; shoot fresh and dry weight (El Mashad and Mohamed, 2012; Jiang et al., 2016b; Chen et al., 2018; Mohamadi and Karimi, 2020; Alharbi et al., 2021; Jiang et al., 2021; Zhang et al., 2021).

Salt stress in apples caused chlorophyll degradation and leaf senescence. However, MEL played an important role in leaf senescence (Shi et al., 2015d; Kul et al., 2019).

Application of melatonin to the seeds of the halophyte *Limonium bicolor* increased gibberellic acid (GA) and alpha-amylase levels and decreased abscisic acid (ABA) levels (Li et al., 2019b).

Under salinity, exogenous melatonin treatment improved shoot dry weight, IAA content, leaf photosynthesis rate, photochemical yield, and chlorophyll values of maximum photosystem II. Melatonin also increased the polyamine content, reducing the degradation of polyamines caused by salt. Melatonin to wheat seedlings under salt stress conditions regulated polyamine metabolism and reduced the effects of salt stress (Ke et al., 2018) while dose-dependently reduced photosynthetic rate and oxidative stress in watermelon plant. While the maintenance of photosynthesis by melatonin application is closely related to the inhibition of stomatal closure in photosystem II and improved light energy absorption and electron transport, the reduction of oxidative stress by melatonin has been linked to improved redox homeostasis with enhanced activities of antioxidant enzymes (Li et al., 2017).

Melatonin alleviated the effects of salinity stress, yield, fruit quality, leaf photosynthetic pigments and macronutrient concentrations. Salinity caused an increase in antioxidant enzymes, abscisic acid and melatonin levels, while foliar application of melatonin further increased these increases. Melatonin application increased leaf antioxidant enzymes and abscisic acid, and decreased salt stress in strawberries (Zahedi et al., 2020). Some researchers emphasized that exogenous treatment of melatonin induces the activities of some antioxidant enzymes, including SOD, POD and CAT, under salt stress, and reduces MDA and electrolyte leakage (Jiang et al., 2016b; Chen et al., 2018; Mohamadi and Karimi, 2020; Park et al., 2021; Wang et al., 2021).

Polyamines (PAs), which are small molecular weight nitrogenous compounds of putrescine (Put), spermidine (Spd) and spermine (Spm), are biomolecules formed in plants in response to stress. PAs have many functions such as plant morphogenesis, reproduction, and delayed leaf senescence. It also has significant effects against abiotic stress conditions such as high and low temperatures, salt, radiation, floods, drought, heavy metals, osmotic stress, ultraviolet. Plant physiological, biochemical and molecular activities increase through interaction with nucleic acids, proteins and phospholipids. Melatonin reduces salinity stress in wheat seedlings by regulating PAs metabolism (Ke et al., 2018; Jahan et al., 2019; Zhan et al., 2019).

Application of 60 µM melatonin to maize under salt stress conditions significantly increased plant growth, chlorophyll content, photosynthesis efficiency, antioxidant enzyme activity and reduced reactive oxygen species (ROS). In addition, coating soybean seeds with MEL significantly increased plant growth and seed yield (Wei et al., 2015). Therefore, it appeared that melatonin treatment to maize seedlings under salt stress conditions has a significant role in reducing the effects of stress (Ahmad et al., 2020). MEL delayed leaf senescence and cell death in rice under salt stress conditions, and increased abiotic stress tolerance by inhibiting the cellular accumulation of H_2O_2 directly or indirectly (Liang et al., 2015).

The structure of melatonin is closely related to IAA (indole−3-acetic acid). Therefore, melatonin, a bio stimulator, provides protection against various abiotic stress conditions such as low temperature, drought and heavy metal stress as well as being effective in root growth, leaf aging and photosynthesis in plants. Melatonin increased salt tolerance in sunflower, soybean, wheat, maize and rice plants. The fact that melatonin increases salt stress tolerance in plants has been attributed to its antioxidant role as a scavenger of reactive oxygen species (ROS) and to the regulation of plant hormones. The first plant melatonin receptor (CAND2/PMTR1) was identified in *Arabidopsis thaliana*. Some studies have shown that melatonin increased stress tolerance through ROS signalling modulated by NADPH oxidase. NADPH oxidase-dependent ROS production conferred tolerance to many types of salinity. NADPH oxidase dependent H_2O_2 signalling increased K^+ uptake in roots of zucchini under salt stress conditions. The increase in salt tolerance with melatonin application rice plant was associated with the ability to retain more K^+ in the root apex region. Salt-induced ROS accumulation is due to the loss of K^+ in plant roots. The decrease in K^+ flow caused by oxidative stress contributes to the increase of K^+ attitude with melatonin application under salt stress (Varghese et al., 2019; Zhan et al., 2019; Liu et al., 2020).

Under salt stress conditions, melatonin caused a significant reduction in the net photosynthetic rate, the maximum quantum yield of PSII, and the total chlorophyll content. Melatonin application in tomatoes, by balancing the distribution of photosynthetic electron flow, reduced ROS production, and facilitated the repair of PSII by protecting the bundle of Psb O and D1. It also improved the ability of PSII to donate electrons and the cleansing ability of ROS by stimulating the activity of enzymes involved in the AsA-GSH cycle (Yin et al., 2019). Similarly, Zhou et al. (2016) demonstrated that MEL reduced ROS level in tomato under salt stress, accelerated the recovery of photosynthetic electron transport chain and protein biosynthesis thus improved photosynthetic capacity under salt stress.

In cucumber, melatonin significantly upregulated the abscisic acid catabolism gene and the gibberellin biosynthetic gene and the down-regulated ABA biosynthetic gene. Therefore, melatonin alleviated the inhibition of NaCl stress on germination by regulating the biosynthesis and catabolism of ABA and GAs. Melatonin eliminated excessively reactive oxygen species, including H_2O_2, but H_2O_2 also regulated melatonin-induced stress tolerance. Exogenous application of melatonin triggered salt tolerance in cucumber. Melatonin improved cell viability, increased the activity of antioxidant enzymes, induced salt stress-related gene expression, protected photosynthesis, reduced malondialdehyde content, and reduced electrolyte leakage of cucumber seedlings under salt stress conditions (Zhang et al., 2020).

In salt stress conditions, application of melatonin to rapeseed caused a decrease in H_2O_2 content (Zeng et al., 2018). Application of 500 µM melatonin to wheat under salt stress was effective in reducing oxidative damage. The increase in antioxidant enzyme activity and biomass production was positively related to yield and revealed the healing effect by upregulating the antioxidative defense mechanism of melatonin in salt stress (Zafar et al., 2019).

Melatonin treatment to cucumber seedlings under salinity conditions improved cell viability, preserved photosynthesis, increased antioxidant enzyme activity, prevented active oxygen explosion and decreased malondialdehyde (MDA) content and relative conductivity. Besides acting as an antioxidant, melatonin also regulates gene expression in many physiological processes. After melatonin application, genes involved in photosynthesis, fatty acid biosynthesis and carbohydrate metabolism were activated in soybean (Wei et al., 2018).

Table 1. Some studies about roles melatonin plays in response to salinity stress in plants

Species	Effects observed	References
Cowpea (*Vigna sinensis*)	improve shoot and root lengths, shoot fresh and dry weights, root fresh and dry weights, number of leaves, leaf area, antioxidant capacity	(El Mashad and Mohamed, 2012)
Maize (*Zea mays* L.)	increase seed germination percentage, seedling vigor index, shoot and dry lengths, seedling fresh and dry weight, relative water content, CAT, POD, proline, total phenolic compounds reduce malondialdehyde (MDA), electrolyte leakage, Na content	(Jiang et al., 2016b)
Maize (*Zea mays* L.)	improve photosynthesis, carotenoid, chlorophyll, relative water content decrease ABA, proline, MDA, electrolyte leakage, Na content	(Chen et al., 2018)
Rosemary (*Rosmarinus officinalis* L.)	enhance plant height, leaf length, new shoot growth length, shoot fresh and dry weight, root fresh and dry weight, SOD, CAT, POD, total chlorophyll reduces electrolyte leakage	(Mohamadi and Karimi, 2020)
Soybean (*Glycine max*)	improve photosynthesis, antioxidant capacity, controlling ion homeostasis, minimism excessive ROS accumulation	(Alharbi et al., 2021)
Green mustard (*Brassica juncea*)	increase plant height, leaf length, leaf width, stem diameter, chlorophyll content, stomatal conductance, photosynthetic rate, transpiration rate, relative water content, CAT, SOD, proline, recover amino acid constituents reduce total phenolic and flavonoid contents, H_2O_2 accumulation	(Park et al., 2021)
Cotton (*Gossypium hirsutum* L.)	increase shoot fresh and dry weight, root fresh and dry weight, proline and chlorophyll content, the maximum photochemical efficiency of PSII (Fv/Fm), ionic homeostasis	(Jiang et al., 2021)
Sweet corn (*Zea mays* L.)	improve SOD, POD, CAT, photosynthesis, transpiration rate, stomatal conductance decreases H_2O_2 accumulation, malondialdehyde (MDA)	(Wang et al., 2021)
Sugar beet (*Beta vulgaris* L.)	increase shoot and root fresh weight, shoot and root dry weight, leaf area, root length, promote photosynthesis, maintain ion homeostasis, removal of ROS, strengthen antioxidant defense system	(Zhang et al., 2021)

The various effects of melatonin on morphological, physiological and biochemical properties under salinity stress have been summarized in Table 1.

Melatonin Promotes Ion Homeostasis under Salt Stress

In salt conditions, application of melatonin controlled the expression of ion channel genes, which was effective in maintaining ion homeostasis and thus increased salinity resistance in plants (Li et al., 2012; Varghese et al., 2019; Zhan et al., 2019).

Ion uptake and partitioning are very important for salt tolerance. Because extreme salt in the cytoplasm disrupts the ion homeostasis and prevents plant growth and development. Melatonin plays an important role in maintaining ion homeostasis. Salt tolerance of M.26 (*Malus domestica*) was increased with melatonin by up-regulation of MdNHX1. Melatonin alleviated the injury caused by high salinity by maintaining ion homeostasis by altering the expression of MdNHX1 and MdAKT1 in apples (Li et al., 2010).

NO played a role in melatonin-enhanced salt stress tolerance in rapeseed. Salinity first caused MEL elevation and served as a downstream signal of NO (Zhan et al., 2019). Melatonin increased the levels of NHX1 and SOS2 transcripts blocked by NO removal. Application of melatonin under salinity affected the degradation and synthesis of ABA [16]. Under salinity conditions melatonin upregulated the NHX1 and AKT1 transporter genes to maintain ion homeostasis (Li et al., 2010; Zhan et al., 2019).

Melatonin Correlated Genes

Salt stress or exogenous melatonin improved intracellular melatonin level, which modulates the expression of genes involved in melatonin biosynthesis and metabolism (Zhan et al., 2019). The protective effect of melatonin application on photosynthetic pigments has been observed in bermudagrass, citrus and sunflower under salt stress conditions. Melatonin application to bermudagrass (*Cynodon dactylon*) under salt stress increased the expression of genes involved in photosynthesis. It also had a positive influence on glucose, fatty acid metabolism and ascorbic acid synthesis (Shi et al., 2015a). The gene expression levels of the PsbO and PsbP subunits of the photosystem I (PSI) related proteins PsaK and PsaG and the PSII photochemical reaction center protein OEC were upregulated by melatonin application. Application of melatonin under salinity increased the level of transcription of genes involved in photosynthesis and preserved the photosynthetic apparatus (Shi et al., 2015b).

One of the most important ways that melatonin regulates the salt tolerance by modulating the activity of transcription factors. The main melatonin-mediated transcription factors in plants are ZAT6, HSFA1s, and

CBF/DREB1s. Multiple stress response genes KIN1, COR15A and RD22 are upregulated by CBF/DREB1, which is closely associated with high melatonin levels, thereby increasing the plant's resistance to salt, drought, and frost stress (Shi et al., 2015c). Melatonin-activated transcription factors regulated the transcription of stress sensitive genes against abiotic stress factors. Similar results were found in cucumber roots under NaCl where melatonin upregulated 77 differentially expressed genes including some important transcription factors. In conclusion, melatonin increased the salt tolerance of plants by regulating the expression of relevant transcription factors (Li et al., 2019a).

Melatonin treatment increased the expression of key genes involved in GA biosynthesis (GA20ox and GA3ox), down-regulated key genes involved in ABA biosynthesis (LbNCED1 and LbNCED3) and up-regulated ABA 8′-hydroxylase genes (LbCYP707A1 and LbCYP707A2) in *Limonium bicolor* (Li et al., 2019b).

Abscisic acid (ABA) and gibberellic acid (GA) are important hormones in stress response of plants. Genes ZEP and NCED1 associated with ABA synthesis were upregulated during abiotic stress, resulting in increased intracellular ABA level (Zhang et al., 2017a). Melatonin mediated ABA biosynthesis and regulation of metabolism, thus decreasing ABA content under stress conditions. Under salt stress, melatonin increased the ABA content in *Elymus nutans*, which was significantly suppressed by fluridone. In salt stress conditions, CsNCED1 and CsNCED2 genes associated with ABA synthesis, transcript levels decreased in seeds with melatonin application and genes related to ABA catabolism increased significantly (Zhan et al., 2019).

Liu et al. (2020) stated that melatonin improves salt tolerance in rice by retaining K^+ in roots and shows that the post-treatment is provided by a simultaneous OsRBOHF-dependent ROS signal that is necessary to melatonin scavenging of hydroxyl radicals and to activate stress-sensitive genes and to increase expression of K^+ uptake carriers at the root tip. Melatonin reduced the sensitivity of salt-induced K^+ flux, a critical determinant of plant salt tolerance, and plasma membrane K^+ permeable channels to hydroxyl radicals, in a dose and time dependent manner. These beneficial effects of melatonin were abolished by the NADPH oxidase inhibitor DPI. Under salt stress, the most noticeable changes in the melatonin-induced root tip are respiratory burst NADPH oxidases, calcineurin B-like/calcineurin B-like interacting protein kinase, and several DEGs encoding calcium-dependent protein kinase was an increase in its expression. Melatonin also enhanced the expression of potassium transporter genes. Melatonin improved salt tolerance in rice by keeping K+ in the roots and the subsequent process demonstrated that hydroxyl radicals were provided by a simultaneous OsRBOHF-dependent ROS signal required to scavenge melatonin and activated stress-sensitive genes and increased expression of K+ uptake transporters at the root tip.

Conclusion

Salt is one of the most serious abiotic environmental factors limiting the yield of plants. Salinity, high temperature, low precipitation, high evaporation rate, poor quality water uses and poor soil management practices increase its impact. Only some of the previous studies on exogenous melatonin application have addressed the effects of melatonin on the recovery of salt stress. To fill this gap, we aimed to investigate how exogenous melatonin treatment affects morphological properties such as plant height, fresh and dry weight, number of leaves, physiological and biochemical properties such as chlorophyll, carotenoid and antioxidant content, phenolic compounds, hormone contents. Accordingly, in this study, the roles of exogenous melatonin to plants under salinity stress in scavenging ROS, regulating the expression of genes associated with antioxidant defense, and therefore removing the germination barrier of seeds, improving cellular ion homeostasis and photosynthetic properties were revealed. For this reason, it has been emphasized that melatonin may contribute to the increase of salt tolerance of plants. The role of melatonin in salt stress is associated with the accumulation of osmotic regulatory substances and the activation of antioxidant enzymes. In future studies, the mechanism by which melatonin increases salt stress tolerance in plants can be investigated in molecular ways and researches can be carried out in field conditions.

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