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Exogenous melatonin ameliorates salinity-induced oxidative stress and improves photosynthetic capacity in sweet corn seedlings

D.Y. WANG, J. WANG, S.H. SHI, L.X. HUANG, M. ZHU+, and F.H. LI+

College of Agronomy, Specialty Corn Institute, Shenyang Agricultural University, 110866 Shenyang, Liaoning Province, China

Abstract

Melatonin (MT) is involved in physiological processes in plants under abiotic stress. In this study, we investigated the effects of melatonin on maize photosynthetic and antioxidant capacities under salinity stress. Our findings indicated salinity stress significantly inhibited maize growth. However, exogenous MT promoted maize growth and antioxidant capacity. Superoxide dismutase, peroxidase, and catalase increased by 138.8, 38.7, and 32.0%, respectively, while H_2O_2 and malondialdehyde decreased by 23 and 31%, respectively. Exogenous MT also improved maize photosynthesis under salinity stress. Net photosynthetic rate, transpiration rate, and stomatal conductance increased by 134, 67.2, and 46.3%, respectively. Maximum quantum yield of PSII photochemistry, effective quantum yield of PSII photochemistry, photochemical quenching coefficient, and electron transport rate increased by 5.8, 70.4, 65.3, and 41.0%, respectively. Therefore, our findings suggested exogenous MT significantly ameliorated maize physiological and photosynthetic adaptation under salinity stress, thereby providing helpful guidance for maize cultivation in areas of high salinity.

Keywords: antioxidant enzymes; gas exchange; melatonin; salt tolerance; sweet corn.

Introduction

Abiotic stress factors have a great impact on agricultural productivity worldwide, of which, soil salinization is the most hazardous (Yu *et al*. 2015). Most crops are vulnerable to an increase in soil salinity; therefore, it is important to develop new strategies to manage salinity stress (Mahajan *et al*. 2020). Several studies have reported a significant decline in growth and biomass yield of plants under salinity stress (Ahanger *et al*. 2018, Alam *et al*. 2019). The effects of salinity stress on photosynthesis have several outcomes. A decrease in stomatal conductance leads to a decrease in carbon dioxide assimilation. Moreover, salinity stress is associated with a decrease in chlorophyll (Chl) content,

Highlights

- Exogenous melatonin (MT) mediated physiological and photosynthetic adaptation in sweet corn
- Exogenous MT maintained the balance of ROS metabolism under salinity stress
- Exogenous MT ameliorated salinity-induced damages of sweet corn seedlings

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+Corresponding author
e-mail: xiaozhu211@syau.edu.cn (M. Zhu)
lifenghai@126.com (F.H. Li)

Abbreviations: APX – ascorbate peroxidase; CAT – catalase; Chl – chlorophyll; C_i – intercellular CO_2 concentration; E – transpiration rate; EDTA – ethylenediamine tetraacetic acid; ETR – electron transport rate; FM – fresh mass; F_v/F_m – maximum quantum yield of PSII photochemistry; g_s – stomatal conductance; MDA – malondialdehyde; MT – melatonin; NPQ – nonphotochemical quenching; P_N – net photosynthetic rate; POD – peroxidase; q_P – photochemical quenching coefficient; ROS – reactive oxygen species; SOD – superoxide dismutase; TBA – thiobarbituric acid; TCA – trichloroacetic acid; WUE – water-use efficiency (= P_N/E); Φ_{PSII} – effective quantum yield of PSII photochemistry.

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damage to the photosynthetic organs, and changes in the activities of enzymes that participate in photosynthesis (Misra *et al*. 1997, Chaves *et al*. 2009).

Ahanger *et al.* (2018) concluded that a decrease in Chl content, net photosynthesis, stomatal conductance, and transpiration was observed in *Solanum lycopersicum* under salinity stress. Besides, Ahmad *et al*. (2019) showed that maximum quantum yield of PSII photochemistry (F_v/F_m), the effective quantum yield of PSII photochemistry (Φ_{PSII}), and photochemical quenching coefficient (q_P) of mung bean plants decreased under NaCl stress, eventually leading to a reduction of photosynthesis. Reactive oxygen species (ROS) are produced when plants are exposed to adverse conditions (Kohli *et al.* 2019). Excessive accumulation of ROS leads to oxidative damage of lipids, proteins, and nucleic acids (Gao *et al*. 2015, Jbir-Koubaa *et al*. 2015), a reduction or loss in enzyme activity, lipid peroxidation of membranes (Bowler *et al*. 1992, Mittler 2002), and disruption of cell membrane integrity (Quintero *et al*. 2007, Farooq *et al*. 2015). There are enzyme-protection systems and nonenzyme-protection systems in plants that help remove a considerable extent of ROS that are produced under abiotic stress, thereby enhancing the adaptation of plants to stress (Allen 1995). The enzymes that are involved mainly include superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APX), and catalase (CAT) (Meloni *et al*. 2003). SOD catalyzes the conversion of $O_2^{\bullet-}$ to O_2 and H_2O_2. The effective removal of H_2O_2 is catalyzed by POD and CAT (Li *et al.* 2018). APX metabolizes H_2O_2 into H_2O and O_2 in plants and plays an important role in maintaining the balance of ROS in cells (Tyagi *et al*. 2020).

Melatonin was discovered in plants in the late 1990s (Zhang *et al*. 2015). It is a tryptophan derivative present in almost all organisms (Sharma and Zheng 2019). Melatonin is an excellent antioxidant, which can regulate the growth of roots, buds, and explants, activate seed germination, and delay leaf senescence in plants (Li *et al.* 2012, Arnao 2014). Previous studies indicate that foliar spray of MT can enhance the total fresh mass and dry mass of wheat plants under cadmium stress (Kaya *et al*. 2019). Melatonin participates in various physiological activities of different crops and protects plants from several abiotic stresses (Lee and Back 2018). Previous studies have reported that melatonin has a positive effect on various plants in alleviating environmental stress (Jiang *et al*. 2016, Liu *et al.* 2018). For instance, exogenous melatonin is known to reduce lipid peroxidation and alleviate cell membrane damage in kiwifruit seedlings subjected to water-shortage stress (Liang *et al*. 2019). In addition, exogenously applied MT has been shown to improve photosynthesis by increasing the content of Chl *a* and *b*, as well as F_v/F_m in the leaves of pepper plants (*Capsicum annuum* L.) subjected to either iron deficiency or salt stress, or in the case of combination stress (Kaya *et al*. 2020). Cucumber seedlings treated with melatonin have been reported to show a high rate of photosynthesis, which alleviates the effect of water stress (Zhang *et al*. 2013). Pretreatment with melatonin inhibits ROS burst, decreases MDA contents, and increases SOD, APX, CAT, and POD activities in tea plants under cold, salt, and drought stress (Li *et al*. 2019). Exogenous melatonin significantly alleviates the inhibition of osmotic stress on the growth of soybean seedlings and gas-exchange parameters. Moreover, the Chl content and photosynthetic rate of leaves were reported to have increased, potentially improving PSII efficiency (Zhang *et al*. 2019, Zou *et al*. 2019). Melatonin pretreatment significantly improves the drought tolerance of wheat seedlings, leading to a reduction in membrane damage and an increase in the rate of photosynthesis compared to the controls (Cui *et al*. 2017). Foliar spraying and direct root application of melatonin have been reported to alleviate damage to the photosynthetic organs and protect tomatoes from low-temperature stress (Yang *et al.* 2018). Some studies have also reported that the widely distributed nonenzymatic small molecule, melatonin, may help directly detoxify and maintain stable concentrations of hydrogen peroxide (Tan *et al*. 2000).

Sweet corn is a subspecies of *Zea mays*, which has excellent characteristics, such as high sugar content, unique flavor, and high contents of several nutrients necessary for the development of the human body. Thus, it is considered an important vegetable and economic crop worldwide (James *et al*. 1995, Feng *et al*. 2008). Sweet corn is easily influenced by high salinity, therefore, it is important to improve the salinity tolerance of sweet corn during cultivation. However, to the best of our knowledge, there are no reports on the alleviation of salinity stress in sweet corn by exogenous melatonin. Therefore, we studied the effects of exogenous melatonin on certain aspects of sweet corn seedlings under salinity stress. Accordingly, in this study, we evaluated the oxidative stress and photosynthetic characters of sweet corn under salinity stress. Further, we explored whether melatonin could improve the salinity stress tolerance of sweet corn seedlings. Additionally, we evaluated the protective role of melatonin in sweet corn seedlings under salinity stress in scavenging ROS, regulating the antioxidant activities of enzymes, and improving photosynthetic characteristics. Our findings could help clarify the alleviation of salinity stress of sweet corn by exogenous melatonin, and also shed light on devising methods for the cultivation of sweet corn in areas of high salinity.

Materials and methods

Plant material and experimental design: *Zea mays* L. *saccharata* Shen Tian No. 8, provided by the Specialty Corn Institute, Shenyang Agricultural Uni-versity, China, was used for this study. This study was carried out in 2020 at the Research and Education Center of Agronomy, Shenyang Agricultural University.

Full, pest-free sweet corn seeds were screened, surface sterilized with 0.5% sodium hypochlorite solution, washed five times with distilled water, and planted in a plug tray with cultivation substrate.

When the seedlings grew to the stage of two leaves, sweet corn seedlings of similar sizes were selected and transferred to a hydroponic container with Hoagland nutrient solution. Concentrations of 100 mM NaCl and

100 μM MT were chosen for the current study based on our preliminary experiments (data not shown) and earlier published reports. For example, Hoagland's solution containing 100 mM NaCl simulates salinity stress in mung bean (Ahmad *et al*. 2019), whereas 100 μM melatonin solution sprayed on Chinese licorice (Afreen *et al*. 2006) and tomato seedlings (Martinez *et al*. 2018) was found to be effective for tolerating abiotic stress. One day after transplantation, an appropriate amount of NaCl was added to the hydroponic container in Hoagland's nutrient solution to cause salt stress at a concentration of 100 mM. The seedlings were divided into the following four groups: (*1*) CK: normal control; (*2*) NaCl: 100 mM NaCl; (*3*) MT: 100 μM melatonin; (*4*) NaCl + MT: 100 mM NaCl and 100 μM melatonin. NaCl at a concentration of 100 mM was added to the hydroponic container of all treatment groups to induce salinity stress. At 17:00 h, seedlings in the MT treatment group were sprayed with 100 μM MT solution, and each hydroponic container was sprayed with 50 mL of this solution. The control group was sprayed with distilled water. All experiments in each group were performed three times. Samples were taken on day 5 of the 100 mM NaCl treatment and the relevant physiological indicators were determined.

Sampling and determination of growth parameters: After NaCl treatment for 5 d, the third fully expanded leaves from the plant bottom were harvested, snap-frozen with liquid nitrogen, and stored at –80°C. Three sweet corn seedlings were randomly selected from each treatment group and washed with water. The aboveground and underground parts were separated. The measured indices included plant height and fresh mass (FM) of the shoots and roots. Next, the shoots and roots were transferred into the respective sample bags, dried in an oven at 105°C for 2 h, and further dried to a constant mass at 80°C. The dry mass (DM) of the shoots and roots was determined.

Gas-exchange parameters: A portable photosynthesis system *LI-6800* (*Li-COR Inc*., Lincoln, NE, USA) was used to measure the photosynthetic parameters of sweet corn seedlings. Photosynthesis of the third fully expanded leaves was measured using three individual plants per treatment. The net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), and intercellular CO_2 concentration (C_i) were measured in a controlled chamber (1 × 3 cm) in an environment of 400 μmol(CO_2) mol^{-1}, 50% relative humidity, and PPFD of 1,500 μmol m^{-2} s^{-1}. Measurements were conducted between 10:00 and 11:00 h. Carboxylation efficiency (P_N/C_i) was calculated based on P_N and C_i, and the water-use efficiency (WUE) of sweet corn seedlings was calculated as P_N/E (Cai *et al*. 2020).

Chlorophyll (Chl) fluorescence: Chl fluorescence was measured using a fluorescence spectrometer (*PAM-2500*, *Walz*, Germany) after the seedlings were allowed to adapt to the dark for 30 min. The maximum quantum yield of PSII photochemistry (F_v/F_m), nonphotochemical quenching (NPQ), the effective quantum yield of PSII photochemistry (Φ_{PSII}), electron transport rate (ETR), and photochemical quenching coefficient (q_P) were measured. Chl fluorescence parameters were calculated according to the method reported by Perera-Castro *et al.* (2018).

Photosynthetic pigment contents: Chl was extracted and analyzed according to the method reported by Lichtenthaler and Wellburn (1983). Briefly, 0.1 g of fresh leaves were chopped finely, soaked in 10 mL of acetone, and left undisturbed in the dark for 48 h. The absorbance at 645 and 663 nm was recorded using a microplate reader (*Multiskan GO*, *Thermo Fisher Scientific*, USA), and acetone was used as a blank. The following formulae were used for calculations: Chl *a* [mg g^{-1}(FM)] = (12.7 × OD_{663} − 2.69 × OD_{645}) × V/(1,000 × M), Chl *b* [mg g^{-1}(FM)] = (22.9 × OD_{645} − 4.68 × OD_{663}) × V/(1,000 × M), Chl (*a*+*b*) [mg g^{-1}(FM)] = Chl *a* + Chl *b*, where OD_{645} and OD_{663} represent the absorbances of Chl at the corresponding wavelengths, V is the total volume of the extract, and M represents the mass of the sample.

MDA and H_2O_2: MDA was measured following the method reported by Hodges *et al*. (1999). Briefly, 0.5 g of fresh leaves were ground with 5 ml of 5% trichloroacetic acid (TCA) in a mortar, and the extract was centrifuged for 5 min at 3,000 × *g*. Next, 2 mL of the supernatant was taken in a 5-mL centrifuge tube and 2 mL of 0.67% thiobarbituric acid (TBA) was added. The sample was mixed well, and the tube was immersed in a boiling-water bath for 30 min and re-centrifuged after cooling. The absorbance of the supernatant was determined at 532, 600, and 450 nm using a microplate reader (*Multiskan GO*, *Thermo Fisher Scientific*, USA). H_2O_2 was measured following the method reported by Xia *et al*. (2009). Briefly, 0.5 g of fresh leaves were homogenized with 5 mL of 0.1% (w/v) TCA in an ice bath. After centrifugation at 12,000 × *g* for 15 min, 0.5 mL of the supernatant was added to 0.5 mL of 10 mM potassium phosphate buffer (pH 7.0) and 1 mL of 1 M potassium iodide. The absorbance of the supernatant at 390 nm was recorded using a microplate reader (*Multiskan GO*, *Thermo Fisher Scientific*, USA).

Antioxidant enzyme activities: About 0.1 g of fresh leaves were homogenized with 5 mL of phosphate buffer (0.05 mM, pH 7.5) containing 0.05 mM EDTA and 2% (w/v) insoluble polyvinylpyrrolidone in an ice bath. For the determination of APX (EC 1.11.1.11), 1 mM of ascorbic acid was added to this mixture. Each homogenate was centrifuged at 1,000 × *g* for 20 min at 4°C and the absorbance of the supernatant was measured using a microplate assay (*Multiskan GO*, *Thermo Fisher Scientific*, USA) to calculate antioxidant enzyme activities. SOD (EC 1.15.1.1) activity was calculated according to the method reported by Abedi *et al*. (2010). Three mL of the reaction mixture containing 14.5 mM methionine, 75 mM NBT, 2 mM riboflavin, 0.1 mM EDTA and 0.1 mL enzyme extract were illuminated for 10 min at a light intensity of 90 μmol m^{-2} s^{-1}. The activity of SOD was determined by

measuring the inhibition of NBT photochemical reduction by enzyme extract at 560 nm. One SOD activity unit was defined as the amount of enzyme needed to inhibit the photochemical reduction of NBT by 50%. The SOD activity was expressed as SOD U mg^{-1}(protein). APX activity was determined according to the method reported by Nakano and Asada (1981). The 3-mL reaction mixture contained 50 mM potassium phosphate buffer (pH 7.8), 0.3 mM ascorbate, 0.06 mM H_2O_2, 0.1 mM EDTA-Na_2, and 0.1 mL enzyme extract, and the absorbance change at 290 nm was measured at 25°C when H_2O_2 was added. One unit of APX activity was defined as 1 μmol of ascorbate oxidized per minute per mg of protein. APX activity was expressed as APX U mg^{-1}(protein). CAT (EC 1.11.1.6) activity was determined using the procedure described by Wang (1995). The activity of POD (EC 1.11.1.7) was measured according to Rao *et al.* (1996) at 470 nm in 2 mL of a reaction mixture containing 100 mM potassium phosphate buffer (pH 6.0), 0.25% (w/v) guaiacol, 0.1 mL of 0.75% (w/v) H_2O_2, and 0.1 mL of enzyme extract. One unit of POD activity was defined as 1 μg of substrate catalyzed per minute per mg of protein. POD activity was expressed as POD U mg^{-1}(protein).

Statistical analysis: All data were analyzed using *IBM SPSS 22.0* and differences between treatment groups were compared using *Duncan*'s multiple range tests at the 0.05 level of confidence using one-way analysis of variance (*ANOVA*). Data are expressed as mean ± standard deviation (SD). Graphs were plotted using *Origin 2019* software.

Results

Plant growth and biomass: Under normal conditions (without salinity stress), the addition of MT had no significant effect on plant height and biomass of sweet corn (Table 1). Salinity stress significantly inhibited the growth of sweet corn seedlings. Compared to CK, the plant height, shoot FM, shoot DM, and root DM were reduced significantly by 14.1, 35, 22.2, and 40%, respectively. On the contrary, spraying the seedlings with exogenous MT effectively improved the growth and biomass accumulation of sweet corn under salinity stress. NaCl + MT treatment resulted in a significant and substantial increase in shoot FM and shoot DM (20.7 and 28.5%, respectively) compared to stress treatment with NaCl alone; root FM and root DM increased by 39.1 and 44.4%, respectively.

Photosynthesis: Salinity stress negatively affected the photosynthesis capacity of the leaves of sweet corn seedlings (Fig. 1). Under salinity stress, the P_N, E, g_s, P_N/C_i, and WUE of sweet corn seedlings were found to decrease by 81.2, 60.5, 58.3, 88.8, and 52.3%, respectively, compared to the control. Nevertheless, the C_i was found to significantly and substantially increase by 68.1% in comparison with the control. However, the application of exogenous MT reversed the inhibitory effects of salinity stress and significantly (P<0.05) increased the P_N, E, g_s, P_N/C_i, and WUE of the seedlings by 134, 67.2, 46.3, 290.9, and 40.4%, respectively, relative to the salinity stress induced by NaCl treatment. The C_i of NaCl + MT was found to decrease by 39.8% in comparison with the NaCl treatment.

Chl fluorescence parameters: The F_v/F_m, Φ_{PSII}, q_P, and ETR of sweet corn seedlings decreased under salinity stress (Fig. 2). Compared with CK, NaCl treatment significantly decreased the F_v/F_m, Φ_{PSII}, q_P, and ETR values by 3.1, 12.1, 30.5, and 39.6%, respectively. The NPQ after NaCl treatment significantly increased by 17.2%. Under normal conditions, there were no significant differences in the fluorescence parameters between the CK and MT groups. However, exogenous melatonin significantly improved F_v/F_m, Φ_{PSII}, q_P, and ETR under salinity stress. Relative to the stress induced by NaCl, treatment with 100 μM melatonin significantly increased the F_v/F_m, Φ_{PSII}, q_P, and ETR by 5.8, 70.4, 65.3, and 41.0%, respectively, suggesting the crucial role of MT in maintaining the efficiency of photosynthesis under salinity stress.

Chl content: Salinity stress significantly decreased the Chl *a*, Chl *b*, and Chl (*a*+*b*) contents by 24.7, 24.3, and 24.6%, respectively, compared to the control (Fig. 3). However, MT treatment alleviated salinity stress and reduced the rate of Chl decomposition. NaCl + MT treatment resulted in a significant and substantial improvement in the contents of Chl *a*, Chl *b*, and Chl (*a*+*b*), which increased by 43.2, 45.6, and 43.9%, respectively, compared to sweet corn seedlings subjected to salinity stress.

H_2O_2 contents and lipid peroxidation: Under normal conditions, there were no significant differences in H_2O_2 and MDA contents between the CK and MT groups. During salinity stress in sweet corn seedlings, high concentrations of H_2O_2 and MDA were determined; however, the

Table 1. Effects of melatonin on the growth and biomass of sweet corn under salinity stress. CK – normal control; NaCl – treatment with 100 mM NaCl; MT – treatment with 100 μM melatonin; NaCl + MT – treatment with 100 mM NaCl plus 100 μM melatonin. Values are expressed as mean ± SD of three replicates. For each variable, means with *different lowercase letters* were significantly different (P<0.05).

Treatment	Plant height [cm]	Shoot fresh mass [g]	Root fresh mass [g]	Shoot dry mass [g]	Root dry mass [g]
CK	28.2 ± 1.48^{a}	1.94 ± 0.33^{a}	1.10 ± 0.33^{ab}	0.18 ± 0.02^{a}	0.15 ± 0.03^{a}
NaCl	24.2 ± 1.09^{c}	1.35 ± 0.16^{c}	0.97 ± 0.29^{b}	0.14 ± 0.01^{b}	0.09 ± 0.01^{b}
MT	27.0 ± 2.22^{ab}	2.02 ± 0.37^{a}	1.22 ± 0.30^{ab}	0.17 ± 0.01^{a}	0.14 ± 0.01^{a}
NaCl + MT	25.9 ± 1.09^{bc}	1.63 ± 0.27^{b}	1.35 ± 0.40^{a}	0.18 ± 0.01^{a}	0.13 ± 0.02^{a}

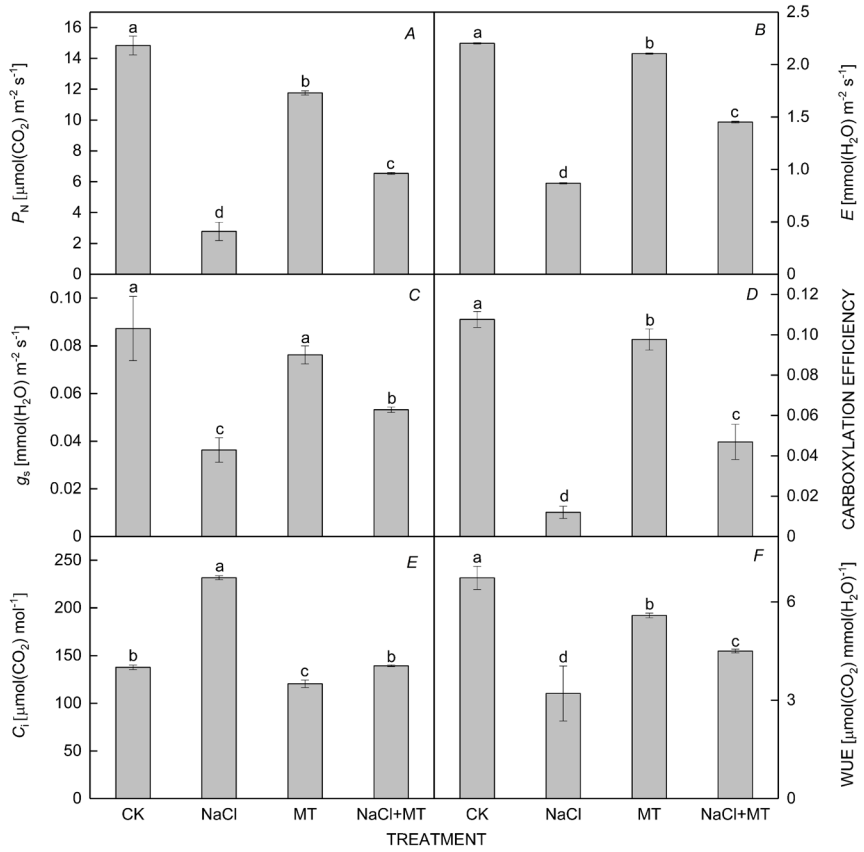

Fig. 1. Effect of melatonin on the net photosynthetic rate (P_N) (*A*), transpiration rate (*E*) (*B*), stomatal conductance (g_s) (*C*), carboxylation efficiency (*D*), intercellular CO_2 concentration (C_i) (*E*), and water-use efficiency (WUE) (*F*) of sweet corn leaves under salinity stress. CK: normal control; NaCl: treatment with 100 mM NaCl; MT: treatment with 100 μM melatonin; NaCl + MT: treatment with 100 mM NaCl plus 100 μM melatonin. Values are expressed as mean ± SD of three replicates. For each variable, means with *different lowercase letters* were significantly different (P<0.05).

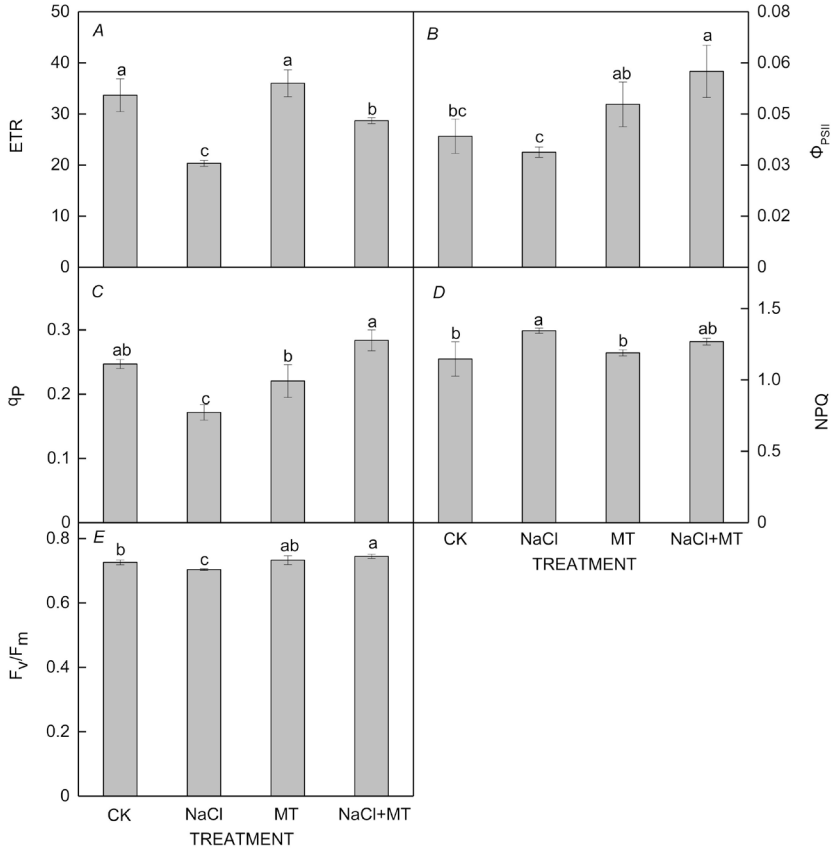

Fig. 2. Effect of melatonin on the electron transport rate (ETR) (*A*), effective quantum yield of PSII photochemistry (Φ_{PSII}) (*B*), photochemical quenching coefficient (q_P) (*C*), nonphotochemical quenching (NPQ) (*D*), and maximum quantum yield of PSII photochemistry (F_v/F_m) (*E*) of sweet corn leaves under salinity stress. CK – normal control; NaCl – treatment with 100 mM NaCl; MT – treatment with 100 μM melatonin; NaCl + MT – treatment with 100 mM NaCl plus 100 μM melatonin. Values are expressed as mean ± SD of three replicates. For each variable, means with *different lowercase letters* were significantly different (P<0.05).

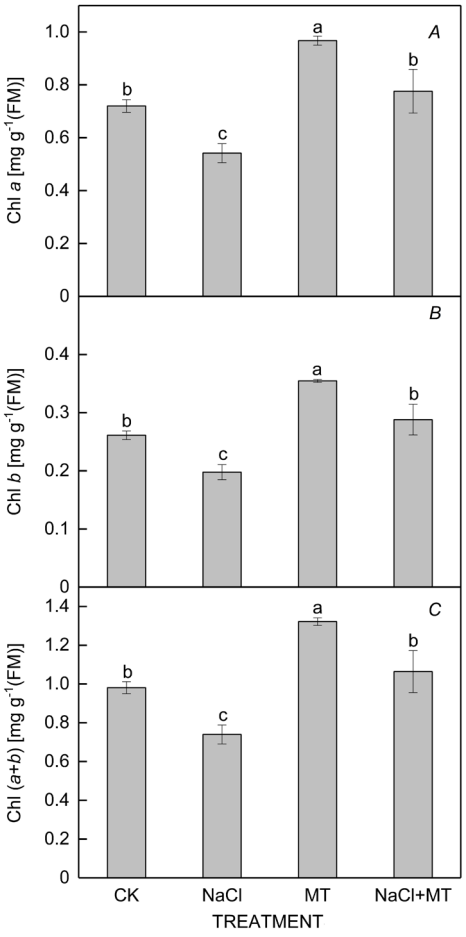

Fig. 3. Effect of melatonin on chlorophyll (Chl) *a* (*A*), Chl *b* (*B*), and Chl (*a*+*b*) (*C*) contents of sweet corn leaves under salinity stress. CK – normal control; NaCl – treatment with 100 mM NaCl; MT – treatment with 100 µM melatonin; NaCl + MT – treatment with 100 mM NaCl plus 100 µM melatonin. Values are expressed as mean ± SD of three replicates. For each variable, means with *different lowercase letters* were significantly different (P<0.05).

accumulation of these compounds was partially reduced after the application of melatonin. The MDA and H_2O_2 contents under salinity stress were significantly higher compared to the control and reached 136.2 and 104.3%, respectively. However, after treatment with melatonin, both MDA and H_2O_2 contents in the NaCl + MT treatment decreased significantly by 31 and 23%, respectively, compared to the seedlings subjected to NaCl stress alone (Fig. 4). These findings indicated that MT application partially but significantly inhibited salinity stress-induced increase in MDA and H_2O_2 in sweet corn seedlings.

Antioxidant enzyme activities: Compared to the control treatment, NaCl stress significantly increased SOD, POD, and CAT activities by 106.8, 87.3, and 72.2% respectively (Fig. 5). Under normal conditions, there were no significant differences in SOD and APX activities between the CK and MT-treated seedlings; however, the activities of POD and CAT in the MT group significantly increased by 68.5 and 51.5%, respectively, compared to those in the CK group. Compared to salinity treatment alone, exogenous MT remarkably increased the SOD, POD, and CAT activities under salinity stress by 138.8, 38.7, and 32.0%, respectively. Moreover, an increase of 2.1% was determined in the APX activities in NaCl + MT-treated seedlings, relative to those treated only with NaCl. These results indicated that SOD, POD, and CAT activities in leaves improved under salinity stress and that external supplementation of MT further enhanced SOD, POD, and CAT activities compared to the seedlings treated only with NaCl. Exogenous MT treatment of sweet corn seedlings did not alter APX activities under normal or salinity conditions.

Discussion

Salinity stress is one of the most common stresses hampering plant growth and restricting crop production on large agricultural lands (Ahammed *et al*. 2018, Kaur *et al*. 2018). It causes ROS imbalance and affects photosynthesis, cell membrane integrity, and enzyme activity in plants (Khaliq *et al*. 2015, Yi *et al*. 2018). In this study, we found that almost all growth parameters decreased significantly

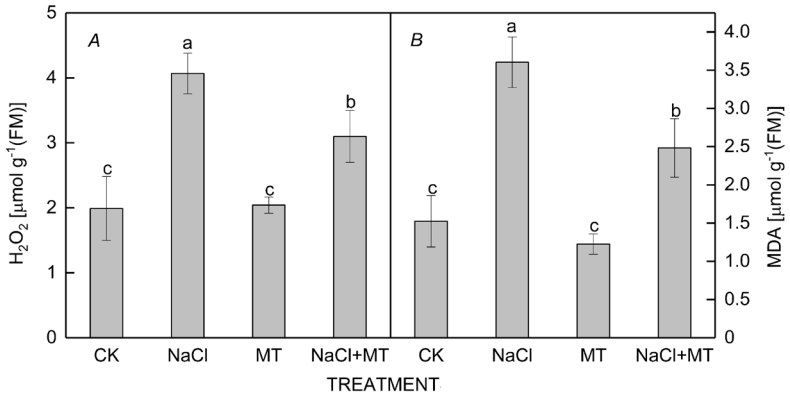

Fig. 4. Effect of melatonin on the H_2O_2 (*A*) and malondialdehyde (MDA) (*B*) contents of sweet corn leaves under salinity stress. CK – normal control; NaCl – treatment with 100 mM NaCl; MT – treatment with 100 µM melatonin; NaCl + MT – treatment with 100 mM NaCl plus 100 µM melatonin. Values are expressed as mean ± SD of three replicates. For each variable, means with *different lowercase letters* were significantly different (P<0.05).

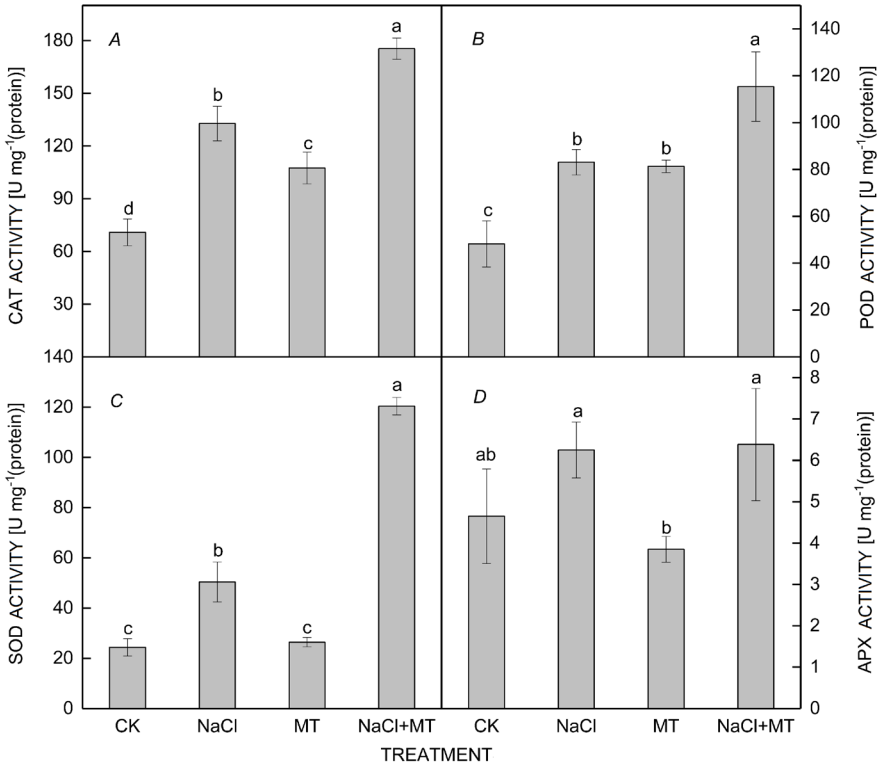

Fig. 5. Effect of melatonin on the activities of catalase (CAT) (*A*), peroxidase (POD) (*B*), superoxide dismutase (SOD) (*C*), and ascorbate peroxidase (APX) (*D*) of sweet corn leaves under salinity stress. CK – normal control; NaCl – treatment with 100 mM NaCl; MT – treatment with 100 μM melatonin; NaCl + MT – treatment with 100 mM NaCl plus 100 μM melatonin. Values are expressed as mean ± SD of three replicates. For each variable, means with *different lowercase letters* were significantly different (P<0.05).

during the NaCl treatment alone, whereas the application of melatonin significantly alleviated the decrease of the shoot and root FM and DM (Table 1). Previous studies suggest that melatonin, as a growth regulator, is related to different abiotic stresses in plants and has a positive effect on the growth of several plants (Arnao and Hernández-Ruiz 2014, Ye *et al*. 2020). We showed that exogenous 100 μM MT could effectively increase the growth, and shoot and root FM and DM of maize under salinity stress. It suggested that exogenous MT possesses the ability to alleviate the salinity stress-inhibited growth and development in maize seedlings to a certain extent.

Plant photosynthesis is a complex physiological process, which is easily affected by environmental conditions (Sterling *et al*. 2019, Zhang *et al*. 2019). The primary limiting factor for photosynthesis upon exposure to salinity is the closure of stomata. Salinity stress leads to a decrease in stomatal conductance, which results in photosynthesis depression (Meloni *et al*. 2003). In this study, salinity stress significantly decreased P_N, E, g_s, P_N/C_i, and WUE, and increased C_i in sweet corn seedlings, indicating that the reason for the decline in photosynthesis was changed from stomatal to nonstomatal limitation, in addition, salinity stress inhibited photosynthetic rate, resulting in excessive absorbed light energy, providing energy for ROS accumulation, thus causing damage to the photosynthetic apparatus, which in turn led to the weakening of carbon assimilation. However, after the addition of exogenous melatonin under salinity stress, C_i decreased significantly, whereas P_N and g_s increased, suggesting that exogenous melatonin could improve stomatal function and the photosynthetic capacity of mesophyll cells under salinity stress, which was consistent with the results of the study by Flexas and Medrano (2002). Moreover, exogenous MT treatment significantly increased E, P_N/C_i, and WUE under salinity stress, indicating its ability to increase the water absorptivity of plants and alleviate the decline in photosynthetic activity under salinity stress. Our results are in agreement with those of Liu *et al*. (2020), who reported a similar increase in these factors in melatonin-treated tobacco seedlings grown under stress conditions.

Chl fluorescence parameters reflect the ability of plants to absorb and transform light energy and help reveal changes in plant gas-exchange parameters (Moghadam *et al*. 2020). Previous studies have shown that exogenous melatonin can improve the light-use efficiency of watermelon under salinity stress (Li *et al*. 2017) and pea under paraquat stress (Szafrańska *et al*. 2016). In the current study, F_v/F_m, q_P, Φ_{PSII}, and ETR of sweet corn seedlings decreased, whereas NPQ increased under salinity stress, indicating that photoinhibition caused by stress and the electron transfer of photosynthetic electrons was blocked, and the efficiency of photosynthetic pigments converting light energy into chemical energy decreased. Pretreatment with exogenous melatonin under salinity stress could improve F_v/F_m, Φ_{PSII}, q_P, and ETR of the leaves of sweet corn seedlings, indicating that exogenous melatonin could improve the photochemical activity of photosystem reaction center of sweet corn seedlings under salinity stress, protect PSII from excessive energy damage, and enhance the stability of photosystem reaction center, which is conducive to the conversion of light energy into chemical energy, thus providing sufficient energy

for carbon assimilation and effectively alleviating the inhibition of photosynthesis in sweet corn seedlings under salinity stress.

Chl is an important component of plants for the conversion of solar energy into chemical energy (Arnao and Hernández-Ruiz 2009); however, Chl is fragile and easily destroyed by ROS (Tan *et al.* 2012). Salinity stress can reduce Chl synthesis and accelerate the decomposition of Chl (Moghadam *et al*. 2020). As a strong oxidant, MT can inhibit the degradation of Chl and maintain the integrity of Chl under conditions of stress. MT treatment can significantly reduce the degradation of Chl in rice leaves under salinity stress, delay leaf senescence, and improve tolerance to salinity stress (Liang *et al*. 2015). In the current study, the Chl content in the leaves of sweet corn seedlings significantly decreased under salinity stress but the Chl content significantly increased with a foliar application of exogenous melatonin. This indicated that exogenous MT treatment enhanced the photosynthetic pigment-synthesis pathway and slowed the decomposition rate of maize leaf Chl under salinity stress.

The cell membrane is selectively permeable to substances, which is the basis of maintaining a normal cellular environment and metabolism. Under stress, excessive free radicals in plant cells can cause lipid peroxidation of membranes and damage the membrane system (Cao *et al.* 2019, Khan *et al*. 2020). An excessive accumulation of ROS occurs during stress in plants. H_2O_2 contents are a suitable indicator to determine the scavenging of ROS under stress (Ahmed *et al*. 2002). MDA is used as an index of lipid peroxidation, which reflects membrane injury (Zhang *et al*. 2014). The accumulation of H_2O_2 resulted in lipid peroxidation, which causes membrane damage (Al-Mureish *et al*. 2014). Melatonin treatment effectively inhibits the accumulation of H_2O_2 and MDA in cucumber seedlings under salinity stress (Wang *et al*. 2016). In our study, we found that H_2O_2 and MDA contents increased under salinity stress, suggesting cell membrane damage; however, H_2O_2 and MDA contents decreased significantly when exogenous melatonin was added under salinity stress. A reduction of H_2O_2 and MDA suggested that exogenous melatonin showed the protective effect against membrane damage under salinity stress.

To reduce oxidative stress, plants possess defense systems to scavenge excessive ROS. The antioxidant enzyme system, comprising SOD, POD, CAT, and APX, is an important system that protects cells from injury, thereby maintaining the balance of ROS in cells, slowing membrane lipid peroxidation, and resisting stress. As an antioxidant, melatonin plays a role in reducing oxidative stress in plants resulting from environmental stress (Rodriguez *et al*. 2004). Choi *et al*. (2011) and Wang *et al*. (2013) suggested that MT could directly scavenge ROS, maintain stable concentrations of H_2O_2, and improve CAT and POD activities. In our study, the SOD, POD, and CAT activities were found to increase significantly under salinity stress. APX activity also increased to a certain extent, but this change was not statistically significant. Moreover, the activities of these enzymes further increased when melatonin was applied under salinity stress. Collectively, our findings suggested that MT may indirectly scavenge H_2O_2 by enhancing the activities of CAT and POD. Our study confirmed that MT was involved in ROS scavenging under salinity stress. It suggested that exogenous MT might protect the plants from abiotic stress and prevent oxidative stress injuries at a cellular level. Therefore, the reversal of salinity stress by MT is attributed to its ability in improving antioxidant capacity and increasing the scavenging of ROS.

Conclusion: Salinity stress negatively influences plant height, biomass photosynthesis, and the chlorophyll fluorescence parameters in sweet corn seedlings. Foliar application of MT at the seedling stage improved photosynthesis, maintained the balance in ROS metabolism, and alleviated the damage caused by salinity stress during plant growth. Together, these results indicated that exogenous MT could alleviate the damage of sweet corn seedlings under salinity stress by enhancing the activities of antioxidant enzymes, reducing oxidative damage, and improving photosynthetic efficiency in leaves. Therefore, pretreatment with exogenous melatonin might be a suitable approach in improving the tolerance of sweet corn seedlings to salinity stress.

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