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Exogenous melatonin alleviates nicosulfuron toxicity by regulating the growth, photosynthetic capacity, and antioxidative defense of sweet corn seedlings

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Abstract

Improper use of nicosulfuron (NSF) may induce harmful effects on plants during weed control. Melatonin (MT) regulates photosynthetic and physiological processes in plants. This study aimed to explore the effects of MT on alleviating NSF toxicity by measuring the growth parameters, photosynthetic capacity, and antioxidative responses in sweet corn seedlings. Compared to NSF alone, exogenous MT increased chlorophyll content, transpiration rate, net photosynthetic rate, stomatal conductance, and maximum efficiency of PSII photochemistry, while reduced malondialdehyde, hydrogen peroxide, superoxide anion radical, and proline contents. Moreover, MT also increased the activity of ascorbate peroxidase and the expression levels of *ZmAPX1*, *ZmAPX2*, *ZmALS1*, and *ZmCYP81A9*. The inhibition of *p*-chlorophenylalanine inhibited the positive effects of MT on photosynthetic and physiological indexes. The results indicated that pretreatment with MT might effectively mitigate NSF toxicity in sweet corn seedlings.

Keywords: antioxidative system; herbicide stress; melatonin; photosystem; sweet corn seedlings.

Introduction

Sweet corn (*Zea mays* L. *saccharata* Sturt) is a subspecies of cultivated corn (*Zea mays* L.). Sweet corn is an essential vegetable grown globally and known for its high sugar content in the endosperm, unique flavor, and nutritional quality. Among various abiotic stress conditions, weed infestation is a crucial factor affecting the quality and yield of sweet corn (Nurjanah *et al.* 2023). Poor weed management significantly impedes the growth of sweet corn, as weeds compete intensely for water and nutrients (Robinson *et al.* 1993). Chemical weeding is currently the most effective and widely used method in crop cultivation. Nicosulfuron (NSF) is a sulfonylurea post-emergence

Highlights

- Nicosulfuron induces oxidative stress and inhibits growth in sweet corn
- Melatonin mitigates nicosulfuron toxicity by improving antioxidant and photosynthetic capacities
- Melatonin increases *ZmALS1* and *ZmCYP81A9* levels and affects target site acetolactate synthase under nicosulfuron toxicity

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Abbreviations: APX – ascorbate peroxidase; CAT – catalase; Chl – chlorophyll; C_i – intercellular CO_2 concentration; CPA – *p*-chlorophenylalanine; *E* – transpiration rate; ETR – electron transport rate; F_v/F_m – maximum efficiency of PSII photochemistry; g_s – stomatal conductance; MDA – malondialdehyde; MT – melatonin; NSF – nicosulfuron; $O_2^{\bullet-}$ – superoxide anion radical; P_N – net photosynthetic rate; POD – peroxidase; PRO – proline; SOD – superoxide dismutase; Φ_{NO} – quantum yield of nonregulated energy dissipation; Φ_{NPQ} – quantum yield of regulated energy dissipation; Φ_{PSII} – effective PSII quantum yield.

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herbicide commonly used in corn production owing to its high safety, efficiency in weed control, low residue, and low dosage (Corbett *et al.* 2005, Chen *et al.* 2023). However, compared to field maize, sweet corn is more susceptible to NSF (Robinson *et al.* 1994, Greenland 2003).

NSF can inhibit acetolactate synthase (ALS, EC 2.2.1.6) in sensitive weeds. This inhibition blocks the synthesis of branched-chain amino acids, such as valine, leucine, and isoleucine, leading to impaired cell division and eventual weed death (Rey-Caballero *et al.* 2016). Moreover, NSF also affects nontarget sites in weeds, including cytochrome P450 monooxygenases (CYP450s), glycosyl-transferases, and glutathione S-transferase (GST) (Yuan *et al.* 2007, Nordby *et al.* 2008). Meanwhile, corn also has an ALS target locus and can experience phytotoxicity if NSF is improperly used, especially in special types such as sweet corn and waxy corn. Improper use can lead to the new-growing leaves of corn seedlings with chlorosis, which may spread to the whole leaf but can gradually recover after about a week (Fontem Lum *et al.* 2005). However, severe NSF toxicity can damage the defense system irreversibly, causing extensive leaf chlorosis and eventually leading to plant death. Studies have demonstrated variations in NSF tolerance among different maize varieties, with field maize exhibiting higher tolerance than that of sweet corn, followed by waxy corn and finally popcorn (Green and Ulrich 1993, Tao and Su 1995). Thus, achieving a balance between effective weed control and avoiding NSF toxicity is a crucial challenge in sweet corn production.

Many studies have demonstrated that plant hormones and growth regulators can improve plant resistance to abiotic stress including alleviating the phytotoxicity of herbicides (Basit *et al.* 2022, Alam *et al.* 2023). For instance, the application of brassinosteroids improved maize tolerance to NSF by scavenging reactive oxygen species (ROS) and increasing the expression of *ZmALS1* and *ZmGST1* (Liu *et al.* 2019). Pretreatment with 0.1 mM salicylic acid (SA) could enhance the ascorbate peroxidase (APX) and glutathione reductase (GR) activities and improve the photosynthetic rate by increasing chlorophyll (Chl) content and electron transfer rate, thereby alleviating the adverse effects of halosulfuronmethyl on soybean (*Glycine max* Merr.) (Li *et al.* 2020). Besides, 1 mM SA minimized the damage caused by prometryne by regulating the activities of GST and mitigating oxidative stress in common beans (*P. vulgaris* L.) (Boulahia *et al.* 2023).

As one of the plant growth regulators, melatonin (MT) can promote plant growth. It stimulates the formation of lateral and adventitious roots, regulates the establishment of dark morphology of plants, boosts seed germination rates, improves fruit quality, affects the flowering time and leaf senescence, and delays post-harvest senescence in fruits and vegetables (Liu *et al.* 2016, Zhang *et al.* 2017, Hu *et al.* 2018, Su *et al.* 2018, Askari *et al.* 2023). Additionally, many studies elucidated the role of MT as a major regulator of biotic and abiotic stresses by ameliorating oxidative damage, modulating gene expression, cross-talking with other molecules, and so on (Li *et al.* 2022, Khanna *et al.* 2023, Shi *et al.* 2023). MT could improve the tolerance of maize seedlings to drought stress by scavenging ROS and promoting stomatal behavior (Ahmad *et al.* 2021, 2022). Pretreatment with MT has been reported to mitigate waterlogging stress in alfalfa by increasing endogenous MT contents and reprogramming polyamine and ethylene metabolism (Zhang *et al.* 2019a). Under freezing stress, foliar-sprayed MT could maintain the structure and mobility of cell membranes in pistachio seedlings, significantly decreasing the active oxygen, sugar, proline, and γ-aminobutyric acid contents (Barand *et al.* 2020). Exogenous MT alleviated the salinity stress-induced oxidative damage in sweet corn by increasing antioxidant enzyme activities and photosynthetic efficiency (Wang *et al.* 2021a). Exogenous MT could also effectively promote nitrogen metabolism-related enzyme biosynthesis in cucumber seedlings under high temperatures (Zhao *et al.* 2012). MT could reduce lead accumulation and eliminate excessive ROS by upregulating the expression of *RsAPX2* and *RsPOD52* and inducing the methylation of *RsGST in vivo* (Namdjoyan *et al.* 2020, Tang *et al.* 2021). MT could improve the tolerance of wheat seedlings to cadmium toxicity by triggering endogenous nitric oxide (Kaya *et al.* 2019). MT increased the resistance of fungal infection of apple plants by increasing the efficiency of PSII, maintaining phenylalanine ammonia-lyase activity, and protecting pathogenesis-related proteins (Yin *et al.* 2013). In addition, the application of MT could alleviate imidacloprid-induced oxidative stress of cucumber by increasing GST content and regulating the ascorbic acid–glutathione (ASA–GSH) cycle, enhancing the activities of key enzymes such as monodehydroascorbate reductase, dehydroascorbate reductase, and GR (Liu *et al.* 2021). Seed soaking with MT could also reduce the accumulation of superoxide anion and protect the photosynthesis of the pea leaves under the phytotoxicity of paraquat (Szafrańska *et al.* 2017). Sweet corn seed primed with MT increased paraquat tolerance by improving the antioxidant enzyme activities and reducing herbicide-induced injury (Fathi *et al.* 2023). However, research on MT alleviating NSF toxicity of sweet corn has not been reported yet.

To address this knowledge gap, this study explored the effects of MT on alleviating NSF toxicity. The main objectives of the study were as follows: (*1*) to determine the concentrations of NSF and MT using super sweet corn hybrids as plant materials; (*2*) to assess whether MT improved photosynthetic capacity under NSF stress by measuring chlorophyll content, gas-exchange parameters, and chlorophyll fluorescence parameters; (*3*) to elucidate the protective role of MT against NSF toxicity in sweet corn by evaluating ROS, membrane lipid peroxidation, and antioxidant enzymes activities; and (*4*) to examine the effects of MT on the expression levels of genes related to *ZmALS1*, *ZmCYP81A9*, *ZmAPX1*, and *ZmAPX2* in sweet corn seedlings under NSF stress. This study revealed the photosynthetic capacity and physiological mechanisms of MT in mitigating NSF toxicity in sweet corn seedlings. It highlighted the potential application of MT in agronomy practices, especially in the safe use of herbicides in sweet corn production.

Materials and methods

Plant materials, herbicides, and reagents: The super sweet corn hybrid Shen Tian no. 8, provided by the Specialty Corn Institute, Shenyang Agricultural University, China, was used in this study. NSF (4% OF) was obtained from *Binnong Technology Co.*, *Ltd*., Shandong, China. MT was purchased from *Yuanye Bio-Technology Co.*, *Ltd.*, Shanghai, China. Additionally, *p*-chlorophenylalanine (CPA), a specific inhibitor of MT synthesis, was purchased from *Ark Pharma Scientific*, *Ltd.*, China.

Experimental design: The experiment was performed in 2021 and 2022, comprising two parts. The first part involved screening the concentration of the NSF and MT as a preliminary experiment, while the second focused on studying the effects of MT on alleviating NSF toxicity in sweet corn. The field experiment was conducted at the Research and Education Center of Agronomy, Shenyang Agricultural University, with no prior history of NSF application.

In the first experiment, sweet corn seedlings at the four-leaf stage were sprayed with NSF at concentrations of 0, 20, 30, 40, 50, 60, 70, and 80 g(ai NSF) ha^{-1}. Simultaneously, MT concentrations of 0, 50, 100, 150, and 200 μM were applied. The growth status of the seedlings was observed in a period of 0–7 d after treatment. Moreover, the morphological and photosynthetic parameters were measured after 7 d. The objective was to identify a concentration of NSF that induced toxicity while allowing the plants to survive. Furthermore, the optimal MT concentration was determined to mitigate NSF toxicity in subsequent experiments.

In the second experiment, the seeds of super sweet corn hybrid Shen Tian no. 8 were selected for uniformity and examined for insect erosion. Uniform-sized seeds with no insect erosion were surface-sterilized with $NaClO_2$ (5%, v/v) for 5 min. After sterilization, sweet corn seeds were rinsed five times with distilled water. Then, the sweet corn seeds were sown in the field. The experiment was conducted in a one-way completely randomized design with three replicates. The row length was 7 m, the row width was 0.6 m, and the plant spacing was 15 cm. In the four-leaf stage of sweet corn seedlings, 150 μM MT and 1 mM CPA containing 0.01% *Tween-20* were sprayed with a hand-held sprayer for three consecutive days until run-off. After 24 h, NSF was sprayed using an electric backpack sprayer. The hybrid seedlings were classified into the following five groups: (*1*) CK (distilled water), (*2*) MT (150 μM melatonin), (*3*) NSF [50 g(ai NSF) ha^{-1}], (*4*) MT + NSF [150 μM melatonin + 50 g(ai NSF) ha^{-1}], and (5) MT + CPA + NSF [150 μM melatonin + 100 μM *p*-chlorophenylalanine + 50 g(ai NSF) ha^{-1}]. Nondestructive photosynthetic indexes were measured on the fifth fully expanded leaf of the plant after NSF treatment for 7 d. Subsequently, the fifth leaves were harvested, snap-frozen with liquid nitrogen, and stored in an ultra-low temperature refrigerator at –80°C for further analysis.

Growth parameters of sweet corn seedlings: The shoot length of seedlings was measured with a metric ruler. After NSF treatment for 7 d, sweet corn seedlings were harvested and the fresh mass was measured using a thousandth balance. The samples were placed in an oven at 105°C for 2 h, and further dried at 80°C to a constant mass for dry mass measurement. The leaf area was calculated with the following formula (Hussain *et al.* 2019): Leaf area [cm^2] = leaf length × maximum leaf width × 0.75 (correction factor).

Chlorophyll (Chl) content: Fresh leaves (0.2 g) were harvested from each treatment with three replicates. All samples were extracted with 15 mL of 95% ethanol and incubated in the dark for 48 h. The absorbance was determined at 645 and 663 nm using a *UV-2550* spectrophotometer (*Shimadzu*, Kyoto, Japan) with 95% ethanol as the blank. The following equations were used to calculate the Chl content (Lichtenthaler and Wellburn 1983): 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*) = Chl *a* + Chl *b*, where OD_{663} and OD_{645} are the absorbances of the extract solution at 663 and 665 nm; V is the total volume of the extract, 15 mL; M is the mass of fresh sample, 0.2 g.

Gas-exchange parameters: A portable photosynthesis system *LI-COR 6800* (*Li-COR*, *Inc.*, NE, USA) was used to measure the net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and transpiration rate (E) in 50% air relative humidity, PPFD of 500 μmol m^{-1} s^{-2}, 400 μmol(CO_2) mol^{-1}, and 25–28°C of air temperature (Wang *et al.* 2021b). Measurements were taken between 10:00–11:00 h after NSF treatment for 7 d.

Chl fluorescence parameters: The maximum efficiency of PSII photochemistry (F_v/F_m), electron transport rate (ETR), effective PSII quantum yield (Φ_{PSII}), quantum yield of nonregulated energy dissipation (Φ_{NO}), and quantum yield of regulated energy dissipation (Φ_{NPQ}) were measured by pulse amplitude-modulated fluorescence spectrophotometer *PAM-2500* (*Walz*, Germany) after 30 min of dark adaptation (Guo *et al.* 2020).

H_2O_2 and $O_2^{\bullet-}$: The content of H_2O_2 and $O_2^{\bullet-}$ were assayed by relative kits (*Solarbio Science & Technology Co*., Beijing, China) according to the instructions.

MDA and PRO contents: The content of malondialdehyde (MDA) was determined by thiobarbituric acid (TBA) method (Hodges *et al.* 1999). First, 1 mL of 10% trichloroacetic acid was added to 0.1 g of corn leaves. The homogenate was centrifuged at 25°C, 4,000 × *g* for 10 min. Then 500 μL of supernatant was fully mixed with 500 μL of thiobarbituric acid. The mixture was incubated at 100°C for 20 min and centrifuged at 25°C, 4,000 × *g* for 10 min. The extract of 200 μL was measured at 532, 450, and 600 nm using a multifunctional microplate reader (*Multiskan GO*, *Thermo Fisher Scientific*, USA).

The proline (PRO) content was determined using the ninhydrin method and based on the original method with slight modification (Troll and Lindsley 1955). First, 0.1 g of sample was ground and mixed with 1 mL of 3% sulfosalicylic acid at 100°C for 10 min, followed by centrifugation at 4°C, 1,000 × *g* for 20 min. The reaction system consisted of 400 µL of glacial acetic acid, 400 µL of acidic ninhydrin, and 400 µL of the sample extract, subsequently bathed in boiling water for 30 min. Toluene of 800 µL was mixed with the solution. Then, 500 µL of the supernatant was centrifuged at 956 × *g*. Finally, 200 µL of the upper red liquid was sucked, the absorbance at 520 nm was measured with a multifunctional microplate reader as mentioned above.

Antioxidant enzyme activities: First, 0.1 g of fresh leaves were homogenized with 500 µL of phosphate buffer (PBS, 50 mM, pH 7.8) and insoluble polyvinylpyrrolidone (PVP). Then, the homogenate was centrifuged for 5 min at 4°C, 15,294 × *g*.

Superoxide dismutase (SOD, EC 1.15.1.1) activity was determined by nitroblue tetrazolium (NBT) method (Abedi and Pakniyat 2010). The reaction system consisted of 50 µL of enzyme solution and 1.5 mL of reaction mixture (containing 14.5 mM methionine, 0.1 mM EDTA, 5 mM nitroblue tetrazolium, and 5 mM riboflavin). Then the mixture was exposed to light for 10 min and OD_{560} was determined rapidly. One unit of SOD activity was defined as the amount of enzyme required to cause 50% inhibition of the reduction of NBT as monitored at 560 nm.

Catalase (CAT, EC 1.11.1.6) activity was measured according to the method of Aebi (1984) with slight modification. First, 100 µL of crude enzyme solution was diluted 11 times with PBS (50 mM, pH 7.8). Then 100 µL of enzyme extract was mixed with 300 µL of 10 mM H_2O_2 and the absorbance of mixture at 240 nm was measured with a multifunctional microplate reader for 4 min. The amount of enzyme decreased by 0.1 in 1 min by OD_{240} was defined an activity unit.

Peroxidase (POD, EC 1.11.1.7) activity was measured by reference to previous report with minor modification (Rao *et al.* 1996). The reaction system consisted of 50 µL of enzyme extract, 1 mL of sodium acetate buffer (100 mM, pH 5.4), 0.5 mL of 0.25% (w/v) guaiacol, and 50 µL of 0.75% (w/v) H_2O_2. The absorbance of mixture at 470 nm was measured with a multifunctional microplate reader for 3 min. The amount of enzyme increased by 0.01 per min by OD_{470} was defined an activity unit.

Ascorbate peroxidase (APX, EC 1.11.1.11) activity was determined by the method of Nakano and Asada (1981). The reaction system contained 50 mM PBS (pH 7.0), 0.1 mM EDTA, 0.3 mM ascorbate, 0.1 mM H_2O_2, and enzyme extract. The reaction solution without enzyme solution was used as the blank control, and the change of absorbance per min at 290 nm was calculated in 3 min. One unit of APX activity was defined as the change of 0.01 per min by OD_{290}.

Related genes expression: The total RNA was isolated from the fresh leaves, and the cDNA template was synthesized by the reverse transcription of RNA using a *MonScript™ RTlll All-in-One Mix* with dsDNase (*Monad Biotech Co., Ltd*., China). The *MonAmp™ ChemoHS qPCR Mix* (*Monad Biotech Co., Ltd*., China) was used for the real-time fluorescent quantitative PCR (qRT-PCR). The *β-actin* was chosen as the internal reference gene. The target genes were *ZmALS1*, *ZmCYP81A9*, *ZmAPX1*, and *ZmAPX2* in this study. The primers of genes (Table 1S, *supplement*) were obtained from previous literature (Liu *et al.* 2015, Wang *et al.* 2018, Liu *et al.* 2019). Three biological repeats were performed for each analysis. The $2^{-\Delta\Delta Ct}$ method was used to calculate the relative transcript levels of the target genes and the internal reference gene.

Statistical analysis: *Microsoft Excel 2016* (*Microsoft*, USA) was used for data consolidation. The data was analyzed by one-way analysis of variance (*ANOVA*) using *SPSS 22.0*. Otherwise, *Duncan*'s multiple range test ($P<0.05$) was used and all results were presented as the means ± standard deviations (SD). Plotting was performed using *Origin 2021* software (*OriginLab*, MA, USA).

Results

Growth parameters: The effects of different NSF concentrations on the growth parameters of sweet corn are presented in Table 1. A concentration of 40 g(ai NSF) ha^{-1} led to a reduction in plant height, fresh mass, leaf area, and dry mass of sweet corn seedlings by 11.3, 14.1, 18.1, and 20.5%, respectively. A concentration of 50 g(ai NSF) ha^{-1} decreased the plant height, leaf area, and dry mass by 18.5, 30.3, and 21.6% compared with untreated control plants, respectively. Moreover, the application of 60, 70, and 80 g(ai NSF) ha^{-1} caused serious malformations of sweet corn seedlings and exhibited a precipitous drop in growth parameters, potentially leading to plant death (Fig. 1S, *supplement*). Based on these findings, the NSF concentration of 50 g(ai NSF) ha^{-1} was selected for the second experiment.

Photosynthetic parameters and growth: The effects of MT concentrations on gas-exchange parameters of sweet corn seedlings under NSF phytotoxicity are presented in Table 2. The results indicated that 50–100 µM MT remarkably increased E, P_N, and g_s of sweet corn seedlings after NSF treatments. The E, P_N, and g_s of NSF + 150 µM MT treatment increased by 165.7, 160.6, and 301.5%, respectively, compared to NSF alone. Furthermore, MT also played a positive role in the growth and development of corn seedlings. Compared with NSF, the increment in plant height, fresh mass, and leaf area for NSF + 150 µM MT, as well as NSF + 200 µM MT, was 21.6, 53.9, and 55.7%, as well as 25.8, 81.6, and 56.0%, respectively. In summary, 150 µM MT was selected for the second experiment.

Chl content: Under non-NSF stress conditions, MT significantly increased Chl *a* and Chl (*a*+*b*) contents by 38.6 and 32.8%, respectively (Fig. 1). Compared

Table 1. Effects of nicosulfuron treatment on the growth of sweet corn under different concentrations. CK – water; NSF – nicosulfuron. Data represent means ± SD of three replicates. *The different letters* in each column are significantly different according to *Duncan*'s multiple range test (P<0.05).

Treatment [g(ai NSF) ha^{-1}]	Plant height [cm]	Fresh mass [g]	Leaf area [cm^2]	Dry mass [g]
CK	88.33 ± 4.62^{a}	57.37 ± 2.64^{a}	926.61 ± 54.95^{a}	7.63 ± 0.41^{a}
20	79.33 ± 2.08^{b}	38.90 ± 2.91^{c}	748.82 ± 25.33^{c}	5.30 ± 0.32^{b}
30	84.00 ± 5.00^{ab}	57.67 ± 8.97^{a}	820.27 ± 65.30^{b}	7.52 ± 1.17^{a}
40	78.33 ± 3.21^{b}	49.30 ± 6.27^{b}	759.04 ± 12.60^{bc}	6.07 ± 0.69^{b}
50	72.00 ± 2.65^{c}	58.23 ± 3.01^{a}	645.93 ± 13.03^{d}	5.98 ± 0.21^{b}
60	48.00 ± 2.65^{d}	28.00 ± 2.67^{d}	290.86 ± 44.64^{e}	3.63 ± 0.16^{c}
70	46.67 ± 2.08^{d}	23.23 ± 2.54^{d}	333.92 ± 16.95^{e}	3.05 ± 0.41^{c}
80	43.67 ± 3.51^{d}	14.43 ± 2.01^{e}	216.31 ± 19.19^{f}	2.10 ± 0.19^{d}

Table 2. Effects of melatonin treatment on the gas-exchange parameters and the growth of sweet corn under different concentrations. Data represent means ± SD of three replicates. *The different letters* in each column are significantly different according to *Duncan*'s multiple range test (P<0.05). E – transpiration rate; g_s – stomatal conductance; P_N – net photosynthetic rate.

Treatment	E [mmol(H_2O) m^{-2} s^{-1}]	P_N [μmol(CO_2) m^{-2} s^{-1}]	g_s [mol(H_2O) m^{-2} s^{-1}]	Plant height [cm]	Fresh mass [g]	Leaf area [cm^2]
CK	3.255 ± 0.122^{b}	34.123 ± 2.291^{a}	0.243 ± 0.017^{b}	163.80 ± 4.80^{a}	520.00 ± 34.39^{a}	4,268.40 ± 414.59^{a}
NSF [50 g(ai NSF) ha^{-1}]	1.364 ± 0.056^{d}	12.041 ± 2.840^{c}	0.072 ± 0.007^{d}	107.20 ± 5.05^{c}	236.57 ± 28.05^{c}	1,779.31 ± 266.38^{c}
NSF + 50 μM MT	2.819 ± 0.060^{c}	20.404 ± 3.917^{b}	0.203 ± 0.016^{c}	106.00 ± 3.97^{c}	278.33 ± 50.00^{c}	1,871.73 ± 337.90^{c}
NSF + 100 μM MT	2.799 ± 0.235^{c}	20.507 ± 3.459^{b}	0.177 ± 0.023^{c}	101.80 ± 3.34^{c}	252.67 ± 15.18^{c}	1,974.24 ± 131.73^{c}
NSF + 150 μM MT	3.623 ± 0.185^{a}	31.377 ± 4.806^{a}	0.288 ± 0.028^{a}	130.33 ± 6.22^{b}	364.00 ± 39.23^{b}	2,769.66 ± 60.540^{b}
NSF + 200 μM MT	3.449 ± 0.195^{ab}	30.099 ± 4.190^{a}	0.205 ± 0.024^{c}	134.80 ± 2.75^{b}	429.57 ± 56.37^{b}	2,775.67 ± 269.11^{b}

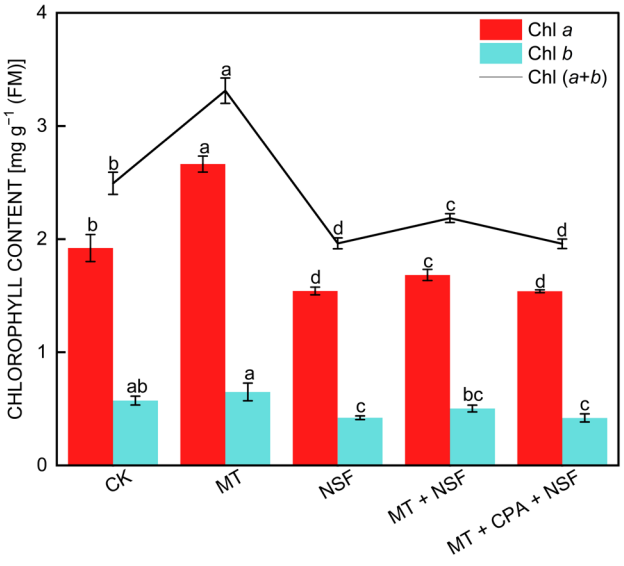

Fig. 1. Effects of melatonin on chlorophyll content of sweet corn under nicosulfuron toxicity. CK – distilled water; MT – 150 μM melatonin; NSF – 50 g(ai nicosulfuron) ha^{-1}; MT + NSF – 150 μM melatonin + 50 g(ai nicosulfuron) ha^{-1}; MT + CPA + NSF – 150 μM melatonin + 100 μM *p*-chlorophenylalanine + 50 g(ai nicosulfuron) ha^{-1}. Data represent means ± SD of three replicates. Means followed by *the different letters* in each column are significantly different according to *Duncan*'s multiple range test (P<0.05).

with the CK, NSF treatment significantly reduced Chl *a*, Chl *b*, and Chl (*a*+*b*) content by 19.8, 26.4, and 21.3%, respectively. However, MT treatment alleviated NSF toxicity and reduced the Chl decomposition rate. MT + NSF treatment resulted in a significant enhancement in the content of Chl *a* and Chl (*a*+*b*), which increased by 9.2 and 11.4%, respectively, compared with NSF. However, the application of CPA could reduce the Chl *a* and Chl (*a*+*b*) contents by 8.6 and 10.4%, respectively, compared to MT + NSF treatment.

Chl fluorescence parameters: Exogenous MT improved the Φ_{PSII} and ETR of sweet corn seedlings compared with the CK. Compared with CK, NSF treatment significantly decreased the F_v/F_m and Φ_{NPQ} by 18.7 and 13.5%, respectively. Additionally, the Φ_{NO} after NSF treatment significantly increased by 26.9% (Table 3). Compared with NSF, MT + NSF significantly increased the F_v/F_m, Φ_{PSII}, and ETR values by 19.2, 71.2, and 73.1%, respectively, while Φ_{NO} decreased by 19.7%. The application of CPA weakened the positive effect of MT, decreasing F_v/F_m, Φ_{PSII}, and ETR by 42.9, 5.5, and 38.4% under NSF stress, or even increased Φ_{NO} by 21.2%.

Gas-exchange parameters: NSF toxicity negatively affected the photosynthetic capacity of sweet corn seedlings (Fig. 2). Under NSF treatment, the transpiration rate (E), net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) decreased by

Table 3. Effects of melatonin treatment on chlorophyll fluorescence parameters of sweet corn under nicosulfuron toxicity. CK – distilled water; MT – 150 μM melatonin; NSF – 50 g(ai nicosulfuron) ha^{-1}; MT + NSF – 150 μM melatonin + 50 g(ai nicosulfuron) ha^{-1}; MT + CPA + NSF – 150 μM melatonin + 100 μM *p*-chlorophenylalanine + 50 g(ai nicosulfuron) ha^{-1}. Data represent means ± SD of three replicates. *The different letters* in each column are significantly different according to *Duncan*'s multiple range test (P<0.05). ETR – electron transport rate; F_v/F_m – maximum efficiency of PSII photochemistry; Φ_{NO} – quantum yield of nonregulated energy dissipation; Φ_{NPQ} – quantum yield of regulated energy dissipation; Φ_{PSII} – effective PSII quantum yield.

Treatment	F_v/F_m	Φ_{PSII}	Φ_{NPQ}	Φ_{NO}	ETR
CK	0.7024 ± 0.0171^{ab}	0.0493 ± 0.0013^{c}	0.5925 ± 0.0663^{a}	0.3311 ± 0.0230^{b}	28.6667 ± 0.6667^{c}
MT	0.7292 ± 0.0174^{a}	0.0732 ± 0.0066^{b}	0.6090 ± 0.0354^{a}	0.3182 ± 0.0327^{b}	44.8333 ± 0.3330^{b}
NSF	0.5710 ± 0.0279^{d}	0.0600 ± 0.0026^{bc}	0.5126 ± 0.0119^{b}	0.4201 ± 0.0228^{a}	35.0556 ± 1.4175^{bc}
MT + NSF	0.6806 ± 0.0153^{b}	0.1027 ± 0.0153^{a}	0.5584 ± 0.0127^{ab}	0.3374 ± 0.0039^{b}	60.6667 ± 9.8330^{a}
MT + CPA+ NSF	0.6432 ± 0.0161^{c}	0.0633 ± 0.0067^{bc}	0.5431 ± 0.0493^{ab}	0.4088 ± 0.0070^{a}	34.6667 ± 0.1667^{bc}

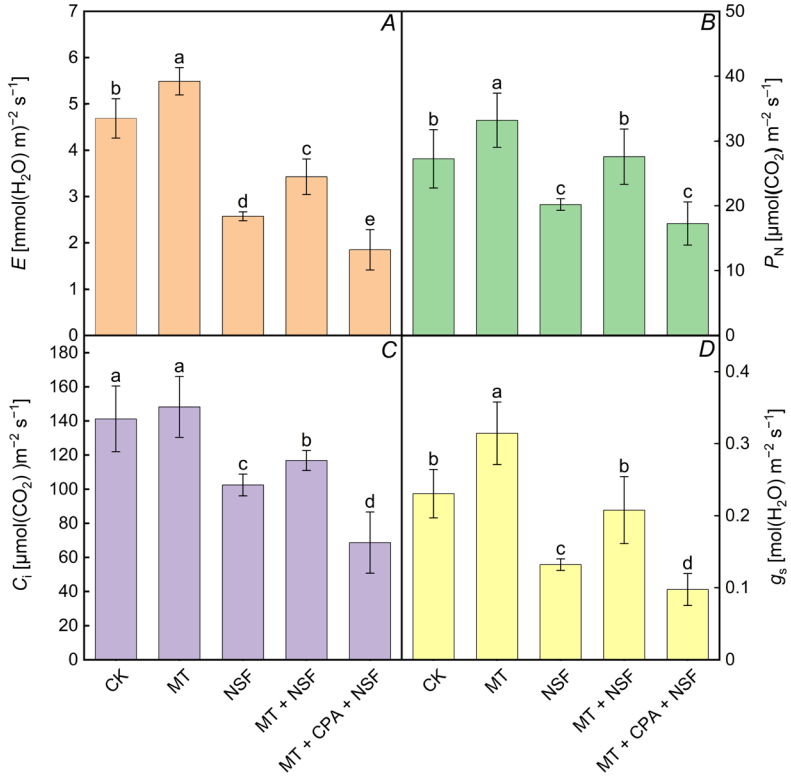

Fig. 2. Effects of melatonin on the gas-exchange parameters of sweet corn under nicosulfuron toxicity. (*A*) Transpiration rate (E). (*B*) Net photosynthetic rate (P_N). (*C*) Intercellular CO_2 concentration (C_i). (*D*) Stomatal conductance (g_s). CK – distilled water; MT – 150 μM melatonin; NSF – 50 g(ai nicosulfuron) ha^{-1}; MT + NSF – 150 μM melatonin + 50 g(ai nicosulfuron) ha^{-1}; MT + CPA + NSF – 150 μM melatonin + 100 μM *p*-chlorophenylalanine + 50 g(ai nicosulfuron) ha^{-1}. Data represent means ± SD of three replicates. *The different letters* in each column are significantly different according to *Duncan*'s multiple range test (P<0.05).

44.7, 25.9, 27.4, and 42.7%, respectively, compared with CK. However, MT + NSF treatment alleviated the NSF toxicity of sweet corn. Compared with NSF, MT + NSF treatment increased the E, P_N, g_s, and C_i by 30.8, 36.6, 14.0, and 57.3%, respectively. On the contrary, CPA had a detrimental effect on sweet corn seedlings under NSF stress, which reduced the levels of E, P_N, g_s, and C_i by 44.1, 37.4, 41.2, and 53.0%, respectively, compared with the MT + NSF treatment.

H_2O_2, $O_2^{\bullet-}$, MDA, and PRO contents: As shown in Fig. 3, foliar-sprayed MT increased the H_2O_2 content of sweet corn seedlings and decreased the MDA content and PRO compared with CK. The increment in the $O_2^{\bullet-}$ content was not statistically significant. However, the $O_2^{\bullet-}$, H_2O_2, MDA, and PRO contents of the plants significantly increased by 101.5, 60.5, 88.1, and 25.2%, respectively, under NSF treatment. Compared with NSF, the contents of $O_2^{\bullet-}$, H_2O_2, MDA, and PRO treated with MT + NSF significantly decreased by 33.2, 16.9, 40.0, and 13.6%, respectively. However, the application of the MT inhibitor CPA accelerated the accumulation of H_2O_2, with its content increasing by 41.8% compared with MT + NSF treatment.

Antioxidant enzyme activities: Under normal conditions, MT increased the SOD activity by 15.7% (Fig. 4). Nevertheless, the activities of SOD, POD, and CAT were enhanced by 28.3, 32.4, and 26.2% compared with the sweet corn subjected to NSF treatment, while the APX activity decreased by 40.9%. Compared with NSF, the SOD, POD, and CAT activities of MT + NSF decreased by 10.9, 16.8, and 27.5%, respectively, and the activity of APX increased by 54.9%. However, CPA did not affect the antioxidant enzyme activities significantly.

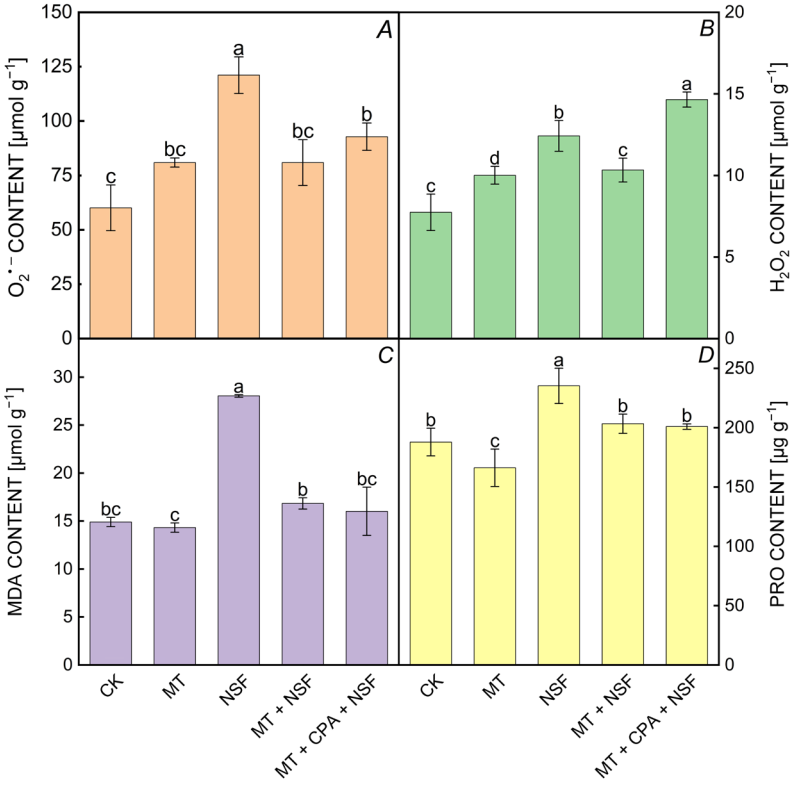

Fig. 3. Effects of melatonin on $O_2^{\bullet-}$ content (*A*), H_2O_2 content (*B*), malondialdehyde (MDA) content (*C*), proline (PRO) content (*D*) of sweet corn under nicosulfuron toxicity. CK – distilled water; MT – 150 μM melatonin; NSF – 50 g(ai nicosulfuron) ha^{-1}; MT + NSF – 150 μM melatonin + 50 g(ai nicosulfuron) ha^{-1}; MT + CPA + NSF – 150 μM melatonin + 100 μM *p*-chlorophenylalanine + 50 g(ai nicosulfuron) ha^{-1}. Data represent means ± SD of three replicates. *The different letters* in each column are significantly different according to *Duncan*'s multiple range test (P<0.05).

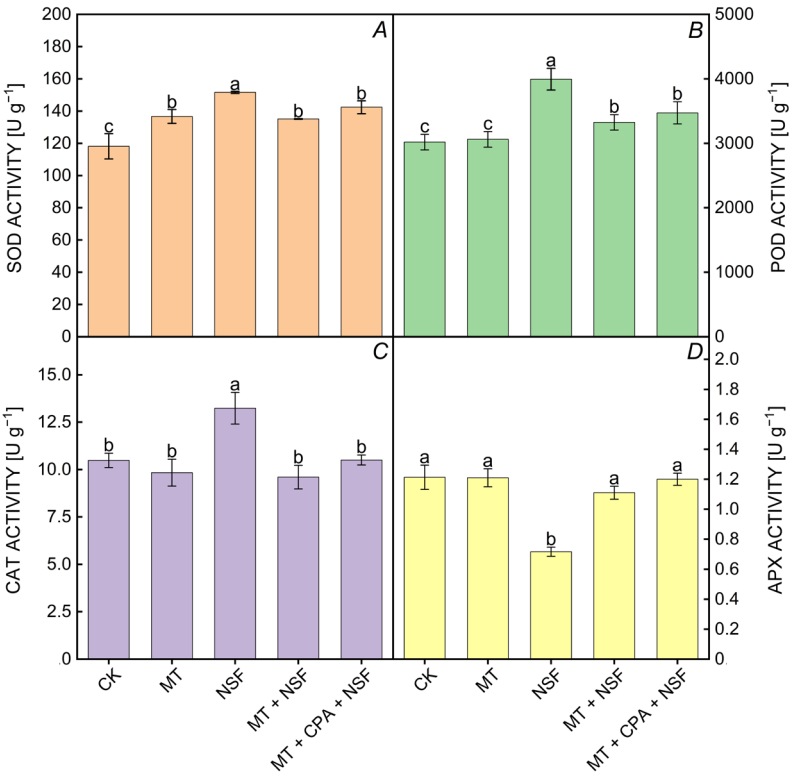

Fig. 4. Effects of melatonin on the superoxide dismutase (SOD) (*A*), peroxidase (POD) (*B*), catalase (CAT) (*C*), and ascorbate peroxidase (APX) (*D*) activities of sweet corn under nicosulfuron toxicity. CK – distilled water; MT – 150 μM melatonin; NSF – 50 g(ai nicosulfuron) ha^{-1}; MT + NSF – 150 μM melatonin + 50 V; MT + CPA + NSF – 150 μM melatonin + 100 μM *p*-chlorophenylalanine + 50 g(ai nicosulfuron) ha^{-1}. Data represent means ± SD of three replicates. *The different letters* in each column are significantly different according to *Duncan*'s multiple range test (P<0.05).

Expression of antioxidant and detoxification genes: As shown in Fig. 5, MT increased the expression of *ZmAPX1* and *ZmAPX2* and decreased the expression of *ZmCYP81A9* by 43.9% compared with CK. However, under NSF stress, the expression levels of *ZmAPX1*, *ZmAPX2*, *ZmALS1*, and *ZmCYP81A9* substantially declined by 63.8, 77.9, 65.8, and 67.1%, respectively. After treatment with MT, the expression levels of *ZmAPX1*, *ZmAPX2*, *ZmALS1*, and *ZmCYP81A9* increased substantially by 74.0, 145.4, 406.8, and 202.8% in plants with phytotoxicity, respectively.

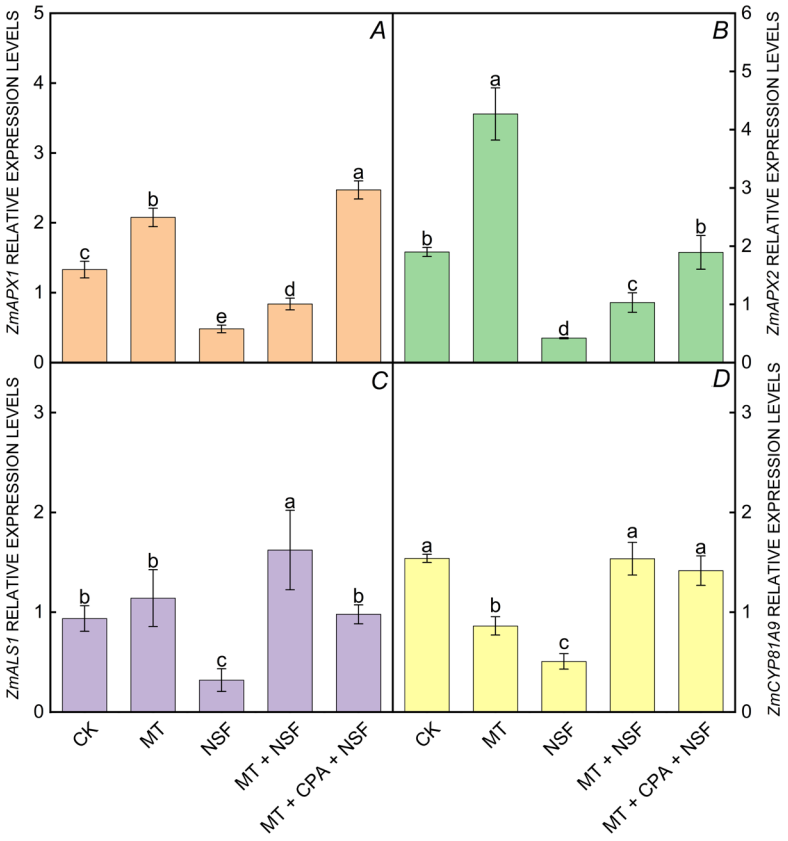

Fig. 5. Effects of melatonin on the relative expression levels of sweet corn related genes under nicosulfuron toxicity. (*A*) *ZmAPX1*, (*B*) *ZmAPX2*, (*C*) *ZmALS1*, and (*D*) *ZmCYP81A9* relative expression levels. CK – distilled water; MT – 150 μM melatonin; NSF – 50 g(ai nicosulfuron) ha^{-1}; MT + NSF – 150 μM melatonin + 50 g(ai nicosulfuron) ha^{-1}; MT + CPA + NSF – 150 μM melatonin + 100 μM *p*-chlorophenylalanine + 50 g(ai nicosulfuron) ha^{-1}. Data represent means ± SD of three replicates. *The different letters* in each column are significantly different according to *Duncan*'s multiple range test (P<0.05).

The application of CPA further promoted the expression levels of *ZmAPX1* and *ZmAPX2* by 194.7 and 83.6%, respectively, and reduced the expression of *ZmALS1* by 39.7% compared with MT + NSF treatment.

Discussion

This preliminary study showed that a high concentration of NSF could reduce plant height, fresh mass, leaf area, and dry mass, as well as gas-exchange capacities of sweet corn leaves (Table 1), which was in direct agreement with previous findings (Sun *et al.* 2017, Liu *et al.* 2019, Wu *et al.* 2022). In addition, 50 g(ai NSF) ha^{-1} could induce phytotoxicity in Shen Tian no. 8 corn seedlings. The preliminary experiment also demonstrated that MT was capable of alleviating NSF phytotoxicity, specifically manifested in its capability to increase the plant height, fresh mass, and leaf area of the plants under NSF phytotoxicity, and enhance the E, P_N, and g_s of sweet corn plants (Table 2).

Photosynthetic capacity: Photosynthesis determines the growth of the plant and is sensitive to abiotic stress, including herbicides (Murata *et al.* 2007, Paul *et al.* 2023). For instance, similar to nicosulfuron, halosulfuron-methyl could inhibit gas-exchange parameters, fluorescence parameters, and chlorophyll content of soybean seedlings (Li *et al.* 2020). In addition, exogenous MT enhanced photosynthesis-related attributes in various stress conditions, as observed in maize, soybean, Chinese hickory, and so on (Zhang *et al.* 2019b, Ren *et al.* 2020, Sharma *et al.* 2020).

As a vital substance in chloroplasts, Chl participates in the absorption and transmission of light energy (Wu *et al.* 2021). Consistent with previous studies, MT significantly increased Chl content under salt and flood stress (Siddiqui *et al.* 2019, Can 2023). The increase in Chl content partly contributes to improved photosynthetic gas exchange (Ahmad *et al.* 2019). In addition, MT has been shown to repair chloroplast structure in maize seedlings (Muhammad *et al.* 2023) and upregulate the mRNA levels of Chl-related genes (*CB12* and *CAB7*) in pepper seedlings (Altaf *et al.* 2023). In this study, the Chl content of plants significantly decreased under NSF stress (Fig. 1). However, MT mitigated the damage of the herbicide to photosynthetic pigments, which was closely associated with a higher plant biomass (Table 2). The use of MT inhibitors reversed the beneficial effect of MT on stress response. These results indicated that MT enhanced the ability of leaves to capture light energy by affecting the Chl content, particularly Chl *a* content, when sweet corn seedlings suffered from NSF toxicity. This enhancement might occur through C_4 pathway-related enzymes or nonenzymatic substances (Wang *et al.* 2021c).

Alternatively, the photosynthetic efficiency of the plant is also closely correlated with stomatal factors (Wang *et al.* 2012). MT could alter stomatal parameters, including length, width, aperture, and area of stomata, thereby ameliorating heat damage in carnation seedlings (Hu *et al.* 2023). Many studies reported that exogenous MT

application positively regulated gas-exchange parameters in strawberries (Khan *et al.* 2023), soybeans (Jahan *et al.* 2023), and lentils (Yasmeen *et al.* 2022) under different stress conditions. This alteration might be achieved through photosynthetic enzyme activity, scavenging of ROS in guard cells, and expression of photosynthesis-related proteins (Kuppusamy *et al.* 2023, Ramasamy *et al.* 2023). In the present study, sweet corn seedlings damaged by NSF significantly reduced g_s (Fig. 2*D*), demonstrating that NSF caused stomatal closure. Further, NSF affected gas exchange by the decline of the E, P_N, and C_i (Fig. 2*A–C*). In contrast, foliar-sprayed MT significantly regulated the photosynthetic activity of the plant in response to NSF stress by increasing the E, P_N, g_s, and C_i. CPA significantly inhibited the improvement in gas exchange induced by MT under NSF treatment. Although the result of MT increasing both g_s and C_i was contrary to a previous study (Lin *et al.* 2022), similar trends have been revealed in some present studies (Huang *et al.* 2019, Sun *et al.* 2023). Therefore, this study hypothesized that MT promoted the stomatal opening and maintained the photosynthetic rate of the plant by accelerating the exchange of gas and water, actively providing photosynthetic raw materials, and ultimately contributing to the rise in E and P_N under NSF toxicity.

Chl fluorescence parameters are commonly used to describe the photosynthetic physiological conditions of plants, reflecting the degree of photosynthetic impact by stress (Bambach *et al.* 2020, Niu *et al.* 2023). Previous studies demonstrated that applying exogenous MT enhanced the photochemical efficiency of PSII under Cd stress and protected PSII from damage induced by chromium stress by controlling electron transfer flow (Ayyaz *et al.* 2020, Zoufan *et al.* 2023). In addition, MT boosted the quantum yield of PSII by promoting linear electron flow and regulating the levels of the photoinhibition-related PSII, O_2 evolution, and excitation energy dissipation proteins under environmental stresses (Lin *et al.* 2022, Ramasamy *et al.* 2023). MT also regulated nonphotochemical quenching by stimulating violaxanthin deep oxidase activity and enhancing the deep oxidation of xanthophyll (Yan *et al.* 2021). In this study, MT significantly increased Φ_{PSII} and ETR of sweet corn seedlings under normal conditions (Table 3), likely as a result of the protective effect of MT on the photosynthetic proteins (Lazar *et al.* 2013). MT also promoted Φ_{PSII}, F_v/F_m, and ETR under NSF toxicity, consistent with a prior study (Lin *et al.* 2022). Moreover, CPA inhibited the positive effect of MT to varying extents. Φ_{NPQ} and Φ_{NO} are essential indicators of photoprotection and photodamage, respectively (Kramer *et al.* 2004). Importantly, this study observed that NSF significantly reduced F_v/F_m and Φ_{NPQ} and increased Φ_{NO}. This result was distinct from drought stress, where MT could depress Φ_{NPQ} and Φ_{NO} (Guo *et al.* 2020). Heat dissipation might be insufficient to support the photoprotection of plants under NSF injury, leading to some electrons being diverted to light quenching. This suggested that NSF stress damaged not only PSII but also threatened the stability of PSI. Fortunately, MT could alleviate light damage under NSF stress and facilitate the orderly transmission of photosynthetic electrons.

Oxidative damage and antioxidant defense system: Several studies have shown that abiotic stress generates a large number of free radicals, which subsequently are converted into ROS (Schützendübel and Polle 2002, Mahajan and Tuteja 2005, Yin *et al.* 2022). The accumulation of ROS not only directly leads to oxidative damage but also indirectly impairs PSI and PSII (Havaux and Davaud 1994, Ahmad *et al.* 2010). Additionally, the MDA content shows the degree of membrane injury induced by oxidative damage as the intermediate product of lipid peroxidation (Vafadar *et al.* 2020). At the same time, PRO accumulates in large quantities to balance cellular osmolytes and maintain cell membrane stability (Hong *et al.* 2000, Sharma and Dietz 2006). MT directly scavenged free radicals and excess ROS by increasing the activity of antioxidative enzymes in many plants such as gerbera, jute, and sorghum (Dey *et al.* 2023, Sher *et al.* 2023, Zulfiqar *et al.* 2023). Different from previous studies, this study found that MT increased the ROS content (Fig. 3*A*,*B*) under non-stress conditions (Yang *et al.* 2020, Ou *et al.* 2023). Li *et al.* (2019) also reported a phenomenon in which 100 μM MT treatment was transiently followed by a significant elevation of $O_2^{\bullet-}$. It might be because the application of MT temporarily disrupted the balance of ROS production and metabolism, but it failed to cause irreversible damage to the plants as the multiple stresses did. Besides, the decrease in MDA and PRO content (Fig. 3C,*D*) might be related to synthetic genes or other active substances (Kaya and Doganlar 2019). Consistent with previous studies, NSF significantly increased the contents of ROS and osmoregulatory substances (Wang *et al.* 2022). The results indicated that NSF caused irreversible membrane damage to the plants. In addition, MT protected the plant from oxidative damage (Khanna *et al.* 2023). In this study, MT reduced the contents of H_2O_2 and $O_2^{\bullet-}$ by declining the accumulation of free radicals, consequently decreasing the concentrations of MDA and PRO by enhancing the stability of the membrane system (Fig. 3). Hence, MT could eliminate the adverse effects of NSF stress on ROS and osmoregulatory substances. Besides, CPA could suppress the beneficial effects of MT under phytotoxicity, which also confirmed the aforementioned speculation.

Plants naturally activate the antioxidant defense system to minimize oxidative damage caused by excessive ROS (Mittler 2002, Ahmad *et al.* 2010). The antioxidant enzyme system, including SOD, POD, and CAT, protects cells from injury by scavenging H_2O_2 and $O_2^{\bullet-}$ (Alscher *et al.* 2002, Ros-Barceló *et al.* 2002). This study showed that sweet corn seedlings responded to NSF stress by increasing SOD, POD, and CAT activities (Fig. 4*A–C*) to scavenge excessive accumulation of ROS, which was consistent with the study by Huang *et al.* (2019). NSF could affect the expression of antioxidant enzyme-related synthetic genes such as *sod9* (Wang *et al.* 2018). MT can

ameliorate oxidative damage by enhancing the activity of antioxidant enzymes under different stresses, similar to what was observed in wheat, sorghum, and tomato (Hasan *et al.* 2015, Al-Huqail *et al.* 2020, Fathi *et al.* 2023). However, this study found that the NSF-induced ROS accumulation was restrained, and the activity of corresponding antioxidant enzymes decreased with the involvement of MT, aligning with previous findings in white beans (Askari *et al*. 2023). This could be attributed to nonenzymatic protection systems (ASA–GSH), which help maintain the redox balance in stressed cells (Kohli *et al.* 2019). APX, as the main enzyme in the ASA–GSH cycle, participates in converting H_2O_2 into H_2O (Gill and Tuteja 2010). NSF significantly reduced the APX activity and MT significantly elevated APX activity under the action of NSF (Fig. 4*D*). This observation confirmed that MT was also involved in the plant's antioxidant defense through a nonenzymatic protection system. However, CPA exhibited no inhibitory effect on APX activity, suggesting that MT might not be the primary regulator in this process and could interact with other substances.

Gene expression levels: MT not only enhanced antioxidant enzyme activity but also affected related gene expression. Studies demonstrated that MT promoted the expression of *APX2*, *GST39*, and *GPX6* in maize under drought stress (Su *et al.* 2018). However, MT significantly reduced the transcriptional profile of antioxidant genes and decreased the expression of stress- and metal sequestration-related genes in tomato seedlings (Raja *et al*. 2023). The altered expression included a reduction in the expression of photosynthesis-related genes and metal chelation-related genes, ultimately mitigating cadmium toxicity. In this study, the expression of *ZmAPX1* and *ZmAPX2* was consistent with the trend of APX activity, suggesting that MT could indeed regulate APX in response to NSF stress by regulating the gene expression of APX (Fig. 5*A*,*B*). However, the abnormal behavior of CPA proved that MT did not play a dominant role in this regulatory relationship. Additionally, ALS activity reflects the resistance of plants to NSF as the target enzyme (Sun *et al.* 2017). The expression of *ZmALS1* substantially decreased under NSF injury, suggesting that the ALS activity of maize was inhibited and the ability of plants to synthesize ALS was seriously threatened (Fig. 5*C*). However, MT alleviated the crisis of plant amino acid synthesis by upregulating the expression of *ZmALS1*. The inhibitory effect of CPA on MT identified that MT could alleviate NSF phytotoxicity by directly acting on the ALS target site. Cytochrome P450 monooxygenases (P450s) provide the molecular basis for herbicide-based weed management through differential gene expression of P450 families, considering the main enzymes involved in herbicide metabolism due to their functional diversity, substrate specificity, and catalytic versatility (Siminszky 2006, Dimaano and Iwakami 2021). Recent studies revealed that NSF resistance in weed populations was mainly conferred by P450-mediated enhanced herbicide metabolism, not by target-gene mutation or overexpression (Wang *et al.* 2023). *ZmCYP81A9* could affect the NSF metabolism as a key member of the P450 family, and its sensitivity and expression level to NSF were higher than those of other members of P450 family (Liu *et al.* 2015). Previous studies showed that *ZmCYP81A9* knock-down in maize led to the loss of plant resistance due to its ability to bind to NSF (Choe and Williams 2020). In this study, exogenous MT could effectively mitigate the decrease in the expression of *ZmCYP81A9* caused by NSF injury in sweet corn seedlings, indicating that MT also indirectly affected the toxic response of NSF by enhancing the nontarget resistance of plants by P450 family (Fig. 5*D*).

Conclusions: The findings revealed that applying 50 g(ai NSF) ha^{-1} induced phytotoxicity in sweet corn seedlings, leading to inhibited plant growth. However, the addition of exogenous 150 μM MT could significantly alleviate the NSF toxicity of sweet corn seedlings. Exogenous MT promoted photosynthetic capacities by increasing chlorophyll content, gas-exchange parameters, and photosynthetic electron transfer rate in sweet corn seedlings. It maintained the balance of ROS metabolism, increased APX activity, and upregulated the expression levels of *ZmAPX1* and *ZmAPX2*. In addition, MT also increased the expression levels of *ZmALS1* and *ZmCYP81A9*, which directly affected the target site ALS of NSF and indirectly promoted the response of plants to NSF toxicity through nontarget sites such as P450. CPA inhibited the positive effects of MT on photosynthetic and physiological indexes in plants. In conclusion, pretreatment with MT may effectively mitigate NSF toxicity in sweet corn seedlings.

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