PLANT SCIENCE TODAY
Vol 12(4): 1-12
https://doi.org/10.14719/pst.11844

eISSN 2348-1900

RESEARCH ARTICLE

Influence of melatonin on salinity tolerance in cowpeas through mitigation of osmotic and oxidative stress

Ibtisam S H AL Khatri, Hamada E Ali & Mahmoud W Yaish*

Department of Biology, College of Sciences, Sultan Qaboos University, P.O. Box 36, Al-khoud, 123 Muscat, Oman

*Correspondence email - myaish@squ.edu.om

Received: 18 September 2025; Accepted: 05 November 2025; Available online: Version 1.0: 19 November 2025; Version 2.0: 04 December 2025

Cite this article: AL Khatri ISH, Ali HE, Yaish MW. Influence of melatonin on salinity tolerance in cowpeas through mitigation of osmotic and oxidative stress. Plant Science Today. 2025; 12(4): 1-12. https://doi.org/10.14719/pst.11844

Abstract

Biostimulators such as melatonin (MT), a plant stress-related phytohormone, enhance plant tolerance to salinity. Therefore, the present study aimed to investigate the ameliorative effects of MT on cowpea plants under salinity stress to determine its mechanism of action and potential application in sustainable agriculture. In this experiment, cowpea seedlings were irrigated with 150 mM NaCl and foliar-sprayed with 300 µM MT as a mitigative treatment. Growth, photosynthetic rate, sodium (Na^+), potassium (K^+), hydrogen peroxide (H_2O_2) and electrolyte leakage (EL) were measured to assess the effects of salinity and MT on cowpea performance. Additionally, osmolytes and both enzymatic and non-enzymatic antioxidants, were evaluated to elucidate the underlying mechanism of MT-mediated salinity mitigation. This study provides the first experimental evidence that 300 µM MT significantly improves cowpea growth and physiological responses under salinity stress. The results showed that plant height and leaf area increased by 32.4 % and 39.4 %, respectively, while fresh and dry weights exhibited only slight improvements. MT application enhanced photosynthesis by 29.4 % and increased anthocyanin content by 37.3 %. Furthermore, MT reduced Na⊠ concentration by about 60 %, lowered EL by 22 % and decreased H_2O_2 levels by 67.4 %. Although potassium levels were unaffected, MT reduced catalase (CAT) activity by 30.6 %. Lastly, total flavonoids increased by 12.1 % under salt stress. Therefore, MT enhances cowpea salinity tolerance by improving photosynthesis, antioxidant defense and ion homeostasis, thereby reducing oxidative damage and serving as an effective biostimulator for cowpeas cultivated under salinity conditions. These findings underscore the potential of MT-enriched bioformulations or organic fertilizers in enhancing crop productivity under salt-affected soils.

Keywords: biostimulators; ion homeostasis; photosynthetic efficiency; reactive oxygen species; *Vigna unguiculata*

Introduction

Salinity is a major abiotic stress that affects plants by inducing water deficit, causing ion toxicity and lowering crop productivity worldwide (1). Cowpea (*Vigna unguiculata*), one of the most widely produced legume crops, is consumed for its grains and fresh green parts, which serve as food for humans and feed for animals due to their richness in protein, vitamin B, folic acid and essential minerals such as iron and zinc, making the crop an important component for human nutrition (2). Cowpeas are relatively tolerant to harsh environmental conditions, including drought, high soil pH, high salinity and temperatures extremes (3). Despite the tolerance, global warming and water scarcity continue to pose significant challenges to cowpea cultivation in saline soils, leading substaintial yield reductions, particularly in arid and semi-arid regions such as Oman. Nevertheless, detailed statistical data quantifying yield losses under saline conditions remain limited.

Salinity stress adversely affects plant growth and development, primarily by reducing biomass and impairing photosynthesis (4). The accumulation of toxic ions, such as Na^+ and Cl^-, disrupts cellular homeostasis, enzyme activity and osmotic balance, leading to ion toxicity and nutrient imbalances (5). High salinity also induces oxidative stress by increasing the production of reactive oxygen species (ROS), which damage lipids, proteins and DNA.

Plants employ various mechanisms to tolerate salinity, including ion compartmentalization, osmotic adjustment and activation of antioxidative defense systems (6). The antioxidative defense process plays a critical role in mitigating oxidative stress, involving enzymes such as superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX), as well as non-enzymatic antioxidants like glutathione, flavonoids and proline (7). These mechanisms help plants maintain cellular integrity and functionality under saline conditions.

The phytohormone melatonin (MT), a molecule associated with regulating sleep in animals, is also synthesized in plants, where it plays a critical role in growth regulation, stress responses and protection against environmental stresses (8). Plants produce MT at high concentrations in response to environmental stresses, such as extreme temperatures, salinity, drought and chemical exposure. MT acts as an antioxidant, aiding plant growth, development and flowering by regulating several plant hormones and increasing phenolic compound

levels (9). Therefore, because some plant tissues naturally contain MT, organic amendments or composts derived from MT -rich plant materials can serve as biofertilizers, offering dual benefits supplying organic nutrients and enhancing plant growth through the physiological actions of MT (10).

Despite the well-documented benefits of MT in improving plant tolerance to various abiotic stresses, its specific role in enhancing cowpea tolerance to salinity remains poorly understood, underscoring the need to explore its potential as a biostimulant to improve crop resilience in saline environments. Therefore, the current study aimed to evaluate the potential of MT to enhance cowpea growth and salinity tolerance by assessing key phenotypic parameters, including plant height and biomass. Additionally, the study aimed to elucidate the underlying mechanisms by which MT mitigates the adverse effects of salinity stress by analyzing various physiological markers, including photosynthetic efficiency and water-use parameters, as well as biochemical indicators such as antioxidant enzyme activity and ion homeostasis.

Materials and Methods

Experimental growth setup and treatments

Cowpea (*Vigna unguiculata* L., subsp. *unguiculata*) seeds of a Canadian cultivar were obtained from the local market in 2021. Four seedlings were grown in synthetic nutrient soil (Hako Potting Substrate) in 4 L pots and irrigated with distilled water for one week. The collection and use of plant materials complied with all relevant regional and national regulations. The pots were separated into four treatment groups: non-saline control, non-saline MT-treated, saline-treated and saline MT-treated. Each group consisted of triplicate samples, with each pot containing a single plant as the biological sample. The saline -treated groups were irrigated weekly with 150 mM NaCl for 2 weeks. The choice of 150 mM NaCl as the salinity stressor in this experiment aligns with previous research, which identified this concentration as a pre-lethal level for plants (11).

A concentration of 300 µM MT was selected for this experiment based on preliminary trials in which multiple MT concentrations were evaluated under salinity stress. This concentration was chosen because it produced the most pronounced beneficial effects at the highest level of non-lethal salt stress. Water solutions of 300 µM MT concentrations were prepared using melatonin powder (Sigma-Aldrich, catalog number M5250). It was applied as a foliage mist to cowpea plants, covering the entire leaf surface to the point of runoff, twice weekly for two consecutive weeks, when grown under optimum (control) conditions and subjected to a salt treatment (150 mM NaCl).

Plants were cultivated in a controlled growth chamber under a 16 hr light and 8 hr dark photoperiod with day and night temperatures of 27 °C and 26 °C, respectively and a relative humidity of 40 % to 45 %. All cowpea seedlings were randomly assigned to four groups. After two weeks of treatment, morphological and physiological traits were measured. This study measured various growth and physiological parameters, including plant height, leaf area, wet and dry weight, photosynthetic pigments, some photosynthesis parameters and electrolyte leakage, to evaluate the effect of MT on the plants.

Assessment of photosynthetic parameters

Measurements of photosynthetic traits were performed between 9:00 am and 11:00 am using LCpro- S.D. (ADS Bioscientific UK). During the measurements, the reference CO_2 concentration was maintained at 400 µmol mol^{-1} and the photosynthetically active radiation was set to 900 µmol m^{2} s^{-1}. The system recorded net photosynthetic rate (*A*), transpiration rate (*E*), stomatal conductance (gs) and intercellular CO_2 concentration (*Ci*). Water-use efficiency (*WUE*) was calculated as the ratio of *A* to *E*.

Quantifying the chlorophylls, carotenoids and anthocyanins

Fresh leaf samples, weighing 0.5 g, were ground in 80 % cold acetone and left in the dark overnight. The resulting mixture was then centrifuged at 5000 g for 15 min and the levels of chlorophyll *a*, chlorophyll *b*, carotenoids and anthocyanidins were determined using a spectrophotometer at wavelengths of 663 nm, 645 nm, 440 nm and 567 nm, respectively. Pigment concentrations (mg/g FW) were calculated based on the previously prepared equations (12):

$$\text{Chl a} = 12.7A_{663} - 2.69A_{645},$$

$$\text{Chl b} = 22.9A_{645} - 4.68A_{663},$$

$$\text{Carotenoids} = \frac{(1000A_{440} - 1.82\ \text{Chl a} - 85.02\ \text{Chl b})}{198}$$

and expressed as mg/g fresh weight.

Root analysis

Root parts of the plants were scanned and analyzed using WinRHIZO (RH-R XLR STD) software (version 5.0, Reagent Instruments, Inc., Quebec, Canada) to measure root length, average diameter, root volume, surface area and the number of root tips.

Measurements of Na+ and K+ leaf concentrations and determine the electrolyte leakage (EL)

The samples were prepared using the previously published method (13). The concentrations of Na^+ and K^+ were quantified using a flame photometer (model 1382, Electronics India, Parwanoo, Himachal Pradesh, India) equipped with a microprocessor, against standards prepared with known concentrations (5 ppm, 10 ppm, 25 ppm, 50 ppm and 100 ppm). The EL was quantified using the previously described protocol (14).

Measurements of hydrogen peroxide (H_2O_2) accumulation

Hydrogen peroxide (H_2O_2) concentration was quantified using the previously established protocol (15). Briefly, 0.2 g of fresh leaf tissue was homogenized in 5 mL of chilled 0.1 % trichloroacetic acid (TCA) and centrifuged at 5000 g for 30 min at 4 °C. The pH of the supernatant was adjusted to 6.8. For the assay, 0.5 mL of the extract was mixed with an equal volume of 0.1 M potassium phosphate buffer (pH 7.0) and 2 mL of 1 M potassium iodide. A blank solution was prepared using 0.1 % TCA without plant extract. The reaction mixtures were incubated in the dark for 1 hr and absorbance was measured at 390 nm. A calibration curve prepared with known concentrations of hydrogen peroxide was used to quantify H_2O_2 and results were expressed as mg g^{-1} fresh weight.

Assessment of antioxidant enzyme activity

The previously established method was used with a few modifications to assess antioxidant enzyme activity (16). Fresh leaf tissue (0.5 g) was homogenized in 5 mL of extraction buffer containing 50 mM phosphate buffer (pH 7.6), 1 mM EDTA and 4 % polyvinylpyrrolidone, maintained at 4 °C. The homogenate was centrifuged at 5000 g for 30 min at 4 °C and the resulting supernatant was collected and stored at 4 °C for antioxidant enzyme activity assays. The APX activity was determined according to the established protocol and the CAT activity was measured by recording the reduction in hydrogen peroxide levels at 240 nm (17, 18). The SOD activity was measured calculated using the equation (19, 20).

Total phenol, flavonoid and glutathione quantification

Total flavonoids and phenols were assessed by the methods by (21, 22). A fresh leaf tissue sample (0.5 g) was powdered in a 5 mL extraction solution and incubated for 2 hr at room temperature. The mixture was then centrifuged at 5000 g for 20 min at 4 ˚C. The total flavonoid content was determined by adding 3 mL of sodium nitrite and 3 mL of 10 % aluminum chloride to 1 mL of extract. The absorbance was measured at 415 nm and a standard curve of catechin was used to calculate the concentration of total flavonoids, expressed in µg/g of fresh weight. For total phenol quantification, 2 mL of 5 % Na_2CO_3 was added to 0.3 mL of the extract following the standard protocol and a standard curve was prepared using reduced glutathione and the total glutathione concentration is expressed in mg/g of fresh weight.

Total soluble sugar determination

The total soluble sugar was determined using the method (23). Leaf tissue (0.2 g) was homogenized in 5 mL of 96 % ethanol and then thoroughly vortexed. The mixture was centrifuged at 3600 g for 10 min and the pellet was incubated in a water bath at 80 °C for 30 min. Equal volumes of the extract and Anthrone reagent (prepared by dissolving 150 mg Anthrone in 100 mL concentrated sulfuric acid) were mixed on ice. The reaction mixture was then boiled for 7 min, cooled to room temperature and its absorbance was measured at 620 nm. A calibration curve prepared from a 100 mg mL^{-1} glucose stock solution was used to determine the total soluble sugar content, expressed as mg g^{-1} fresh weight.

Proline content measurement

Proline content was quantified according to the previously described method, with a few minor modification (24). Fresh leaf tissue (0.5 g) was homogenized in 3 mL of 3 % sulfosalicylic acid and centrifuged at 5000 g for 30 min. To 0.2 mL of the supernatant, 0.8 mL of acid ninhydrin and an equal volume of glacial acetic acid were added. The reaction mixture was incubated in a boiling water bath (90 °C) for 1 hr, after which 1.6 mL of toluene was added, resulting in phase separation. The toluene phase was collected and absorbance was measured at 520 nm with a spectrophotometer. Proline concentration was determined using a standard curve prepared with L-proline and expressed as µg g^{-1} fresh weight.

Statistical analysis

The data were analyzed with SPSS software. A one-way ANOVA was conducted at a *P*-value of ≤ 0.05 to determine the significance level, followed by LSD to determine the significance between treatments.

Result

MT mitigates the growth of cowpea plants under salinity

Various growth and physiological parameters were measured to assess the impact of MT on the plants. Additionally, several biochemical assays were performed, including the measurement of H_2O_2 accumulation, the activities of APX, CAT, SOD and the determination of soluble sugar, proline, phenol, flavonoid and glutathione contents. Overall, cowpea plants showed a clear decline in growth when exposed to salinity, with symptoms of weakness and wilting; however, the external application of 300 µM melatonin improved their tolerance to salt stress and enhanced growth performance (Fig. 1).

Watering cowpea seedlings with a 150 mM NaCl solution significantly ($P \leq 0.05$) reduced plant height by 36.6 % and leaf area by 41.4 %. Under control conditions, applying MT insignificantly increased plant height and leaf area by 16.2 % compared to untreated plants (Fig. 2A, B). However, under saline conditions, the exogenous application of 300 µM MT significantly ($P \leq 0.05$) enhanced plant height by 32.4 % and leaf area by 39.4 % compared to plants grown under saline conditions without MT treatment.

The harmful effects of salinity on cowpea biomass were apparent, as it caused a significant ($P \leq 0.05$) reduction in both fresh weight (53.21 %) and dry weight (50.3 %) compared to control plants. Under normal conditions, MT application significantly increased cowpea biomass ($P \leq 0.05$), with fresh weight rising by 35.0 % and dry weight by 39.0 %. However, under saline conditions, MT application only slightly enhanced the fresh and dry weight of cowpea plants (Fig. 2C, D).

The root system was analyzed to evaluate the impact of salinity and MT on root architecture. The results showed that exogenous application of MT under non-saline conditions

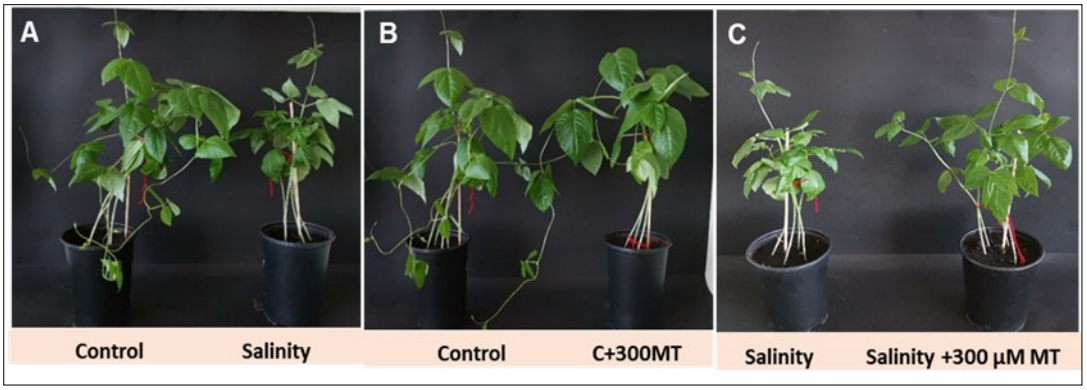

Fig. 1. Phenotypic changes in cowpea plants under various treatments: 150 mM NaCl solution (salinity) (A), 300 µM MT treatment under non-saline conditions (C + 300MT) (B) and 300 µM MT treatment under saline conditions (C + 300 MT) (C).

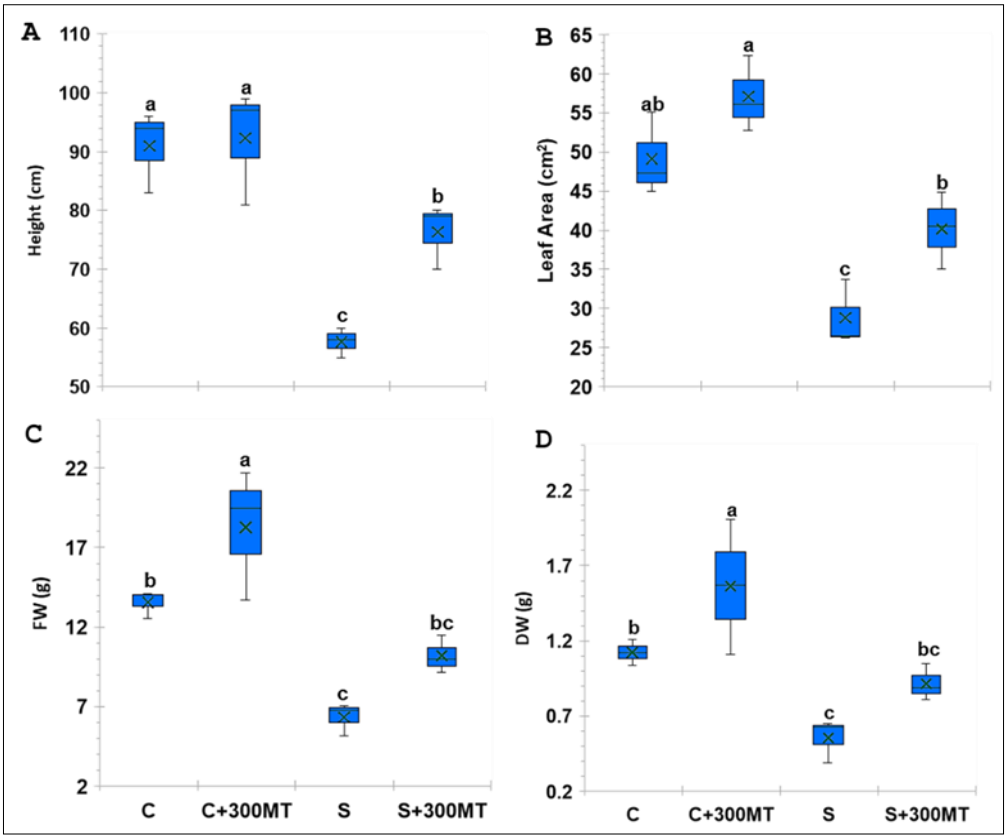

Fig. 2. The effects of exogenous application of 300 µM MT on plant growth characteristics under control and salt conditions, including the plant height (A), the leaf area (B), the fresh weight (C) and the dry weight in cowpea plants of the above-ground tissues (D). Boxplots with different letters are significantly different ($P \leq 0.05$, n =3) among treatments, as evaluated by the LSD test.

significantly ($P \leq 0.05$) enhanced several root growth parameters, including root length, surface area and volume. However, MT treatment did not significantly affect the average root diameter and root tip number (Fig. 3A,-C, E). Interestingly, the root volume increased 48.5 % under non-saline conditions (Fig. 3D). Under salinity, root length, surface area and the number of root tips were significantly ($P \leq 0.05$) reduced; for example, root length and surface area decreased by 37.3 % and 25.4 %, respectively, compared to control plants (Fig. 3A, B). However, the root volume was unaffected by salinity (Fig. 3). While average root diameter remained unchanged under both salt stress and MT treatment, exogenous MT application significantly ($P \leq 0.05$) improved root architecture parameters under saline conditions by increasing the number of root tips by 59.7 % compared to salt-stressed plants without MT treatment (Fig. 3C, E).

MT relieves the salinity effect on the photosynthesis system

MT application did not alter intercellular CO_2 concentration (*Ci*) under either control or saline conditions; however, *Ci* decreased significantly under salinity stress ($P \leq 0.05$) by 12.2 % under salt stress compared to control conditions (Fig. 4A). The transpiration rate (*E*) also decreased significantly ($P \leq 0.05$) by 32.8 % under salt stress compared to the control (Fig. 4B). Under non-saline conditions, MT treatment significantly ($P \leq 0.05$) increased *E* by 10 %. However, under saline conditions, MT treatment significantly ($P \leq 0.05$) increased *E* by 30 % compared with salt-stressed plants that did not receive MT. Similarly, stomatal conductance (*Gs*) decreased significantly ($P \leq 0.05$) by 50.2 % under salinity conditions compared to the control (Fig. 4C). While MT treatment under control conditions did not substantially affect *Gs*, it increased Gs by 60 % in salt-stressed plants compared to untreated plants. Salinity treatment significantly reduced the photosynthetic rate (*A*) and showed a slight decrease with MT application under non-saline conditions. However, under salt stress, MT application significantly ($P \leq 0.05$) improved *A* by 29.4 % compared to salt-stressed plants without MT treatment (Fig. 4D).

The effect of MT on water use efficiency (WUE) was evaluated in cowpea plants grown under both control and salinity conditions. The results indicated that WUE was significantly ($P \leq 0.05$) improved by 21.7 % under salinity conditions compared to the control (Fig. 4E). However, while MT treatment had no significant effect on WUE under salt stress, it significantly ($P \leq 0.05$) reduced WUE by 13.7 % under non-saline control conditions.

To evaluate the potential protective role of MT on these pigments, chlorophyll a, chlorophyll b, carotenoids and anthocyanins were measured. The results showed minimal changes in chlorophyll concentrations between the control and salt-treated groups. Under non-saline conditions, exogenous MT application did not significantly affect chlorophyll a, chlorophyll b, carotenoids and anthocyanins. However, under salt stress, MT application significantly increased ($P \leq 0.05$) anthocyanin content by 37.3 % compared to the salt treatment alone (Fig. 5).

MT reduces Na^+ accumulation and moderates the electrolyte leakage under salinity

$Na^+$and K^+ ion concentrations were measured to evaluate the impact of MT on the ion accumulation in cowpea leaves under both control and salinity conditions. The results showed that under non-saline conditions, MT application reduced Na^+con centration to an average of 0.05 mg g^{-1} DW, compared to 0.25 mg g^{-1} DW in untreated control plants; however, this reduction was not statistically significant (Fig. 6A). Under saline conditions, the Na^+concentration significantly increased (P ≤ 0.05) to four times the level observed in the control. Interestingly, the MT application under salinity significantly ($P \leq 0.05$) reduced Na^+concentration to 0.4 mg g^{-1} DW.

The results showed that salinity and MT treatment had an

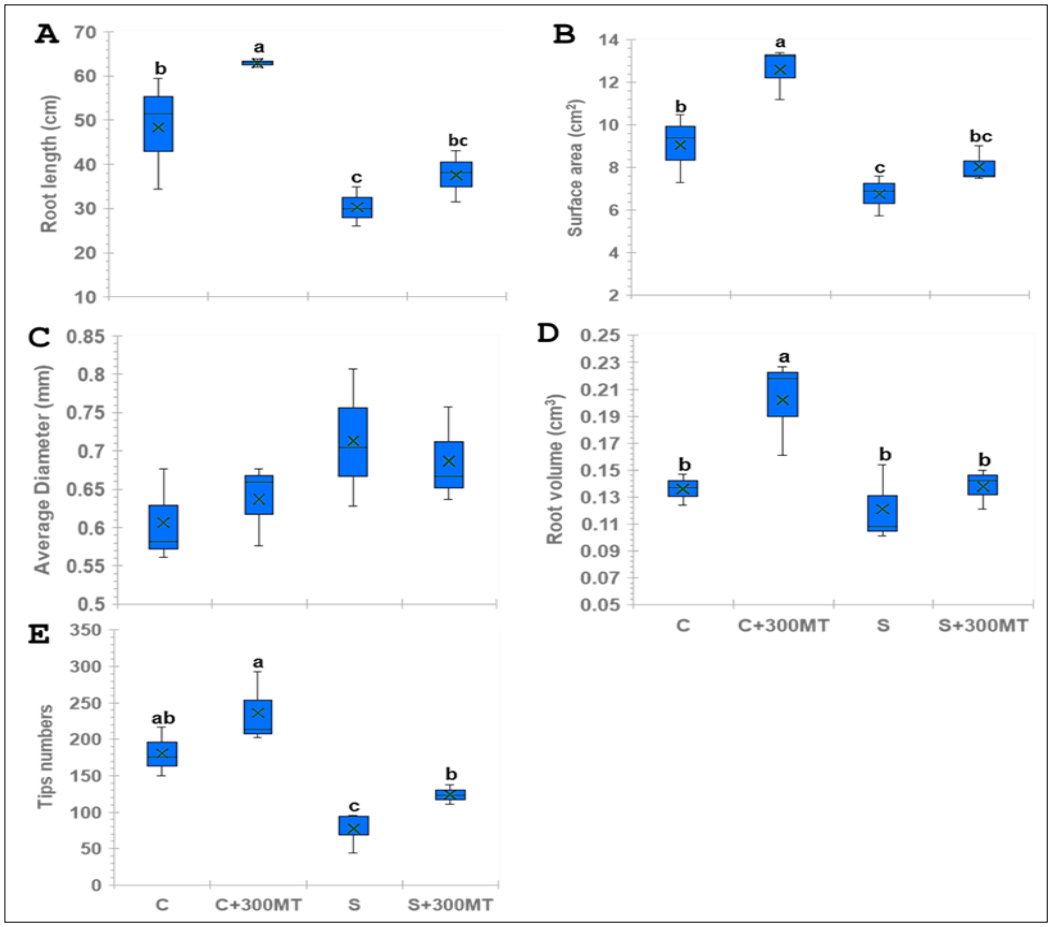

Fig. 3. The effect of salinity and MT treatment on root length (A), root surface area (B), average diameter (C), root volume (D) and number of tips (E) in cowpea plants. Boxplots with different letters indicate significant differences ($P \leq 0.05$) among treatments as determined by the LSD test.

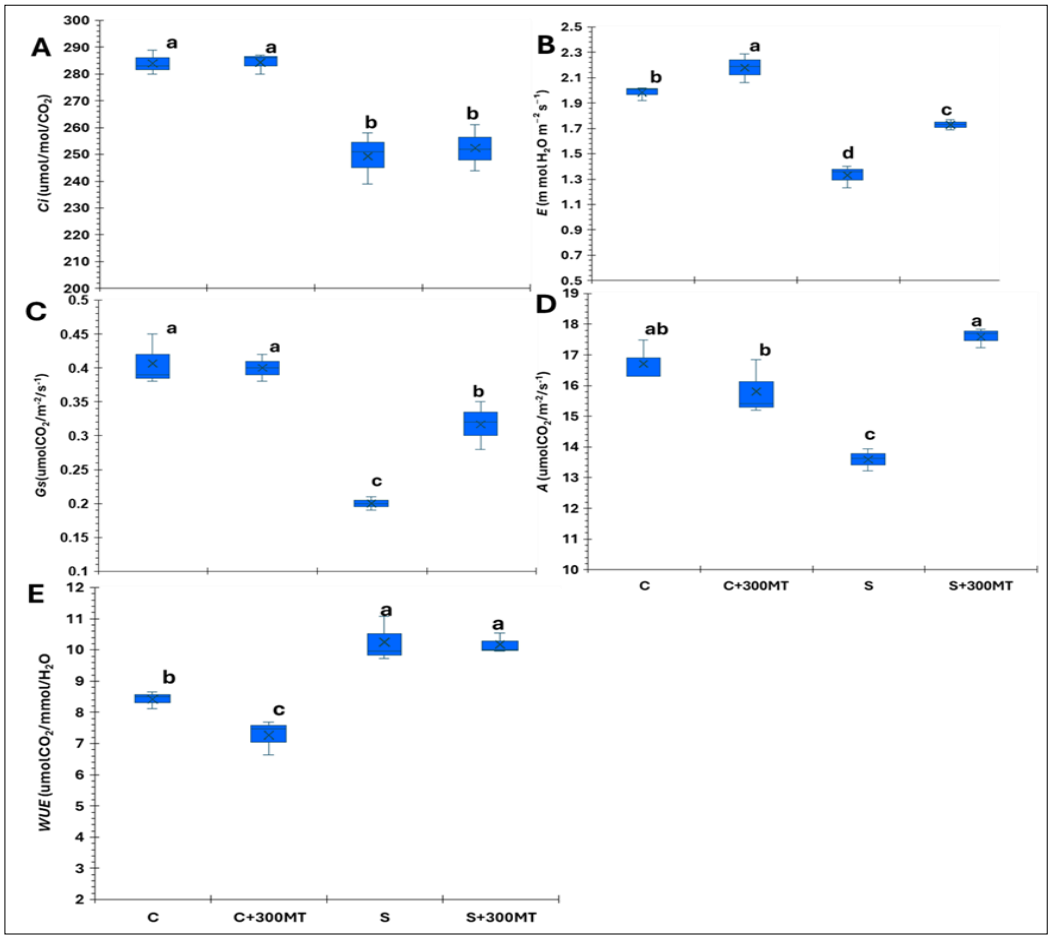

Fig. 4. Effect of salinity and 300 µM MT application on intercellular CO_2 concentration (*Ci*) (A), transpiration rate (*E*) (B), stomatal conductance (*Gs*) (C), photosynthesis rate (*A*) (D), water use efficiency (*WUE*) (E) in cowpea plants. Boxplots with different letters indicate significant differences ($P \leq 0.05$) as determined by the LSD test.

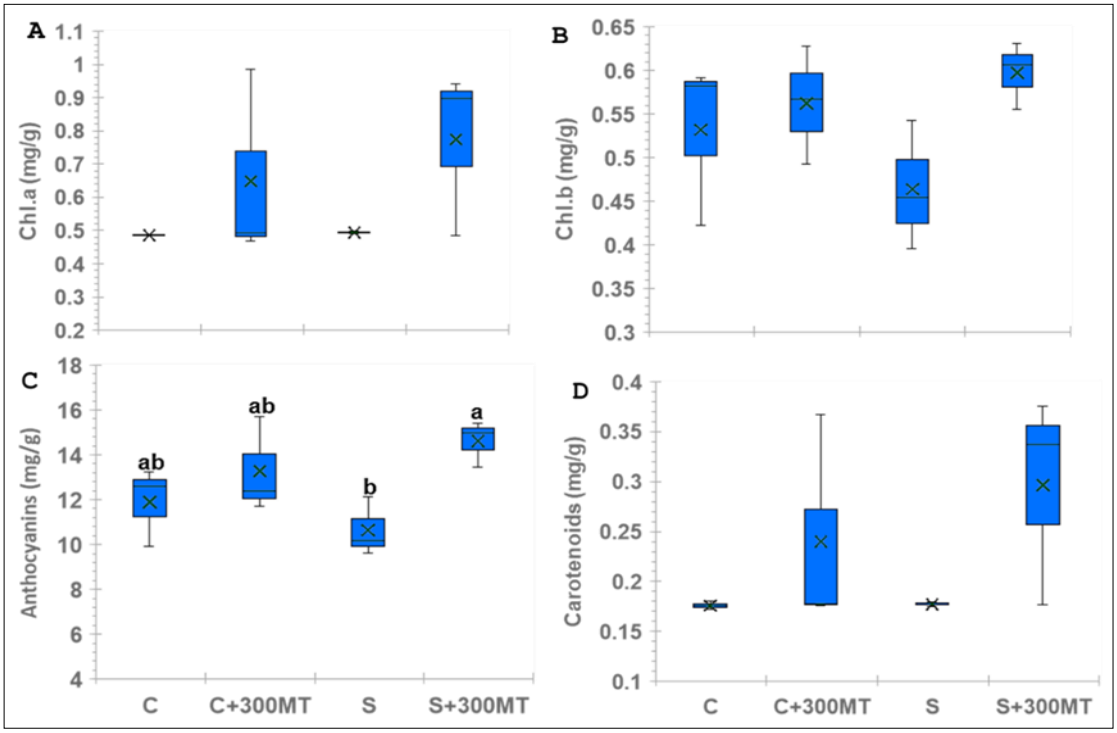

Fig. 5. The effect of 300 µM MT application on photosynthetic pigments was assessed under both control and salt conditions, revealing changes in chlorophyll a (A), chlorophyll b (B), anthocyanins (C) and carotenoid content (D) in cowpea plants. Boxplots with different letters are significantly ($P \leq 0.05$) different, as evaluated by the LSD test.

insignificant effect on K^+concentration in cowpea plants, with no statistically significant differences observed between the control and treatment groups (Fig. 6B). However, the Na^+/K^+ ratio was significantly higher under salt stress but decreased substantially with MT treatment (Fig. 6C).

Salinity stress can damage plant cell membranes, causing increased ion leakage. Plants with high salt tolerance can better maintain lower ion leakage levels. In cowpea plants subjected to salt stress, EL was significantly ($P \leq 0.05$) higher, increasing by 21.2 % compared to the control group (Fig. 6D). However, applying MT under salinity conditions significantly ($P \leq 0.05$) reduced Na^+ accumulation, leading to an average 22 % reduction in EL.

MT exhibits no significant impact on soluble sugar and slightly reduces proline under salinity

Under salt stress, plants accumulate elevated levels of soluble sugars and proline, which serve as adaptive components of their tolerance mechanism. Our results indicated an insignificant difference in soluble sugar levels between cowpeas grown under salinity and control conditions (Fig. 7A). Similarly, the MT application did not significantly affect soluble sugar production under either condition. In contrast, proline levels increased significantly ($P \leq 0.05$) by 78.3 % in salinity-treated plants compared to control plants (Fig. 7B). However, MT treatment under saline conditions reduced proline levels by 24.6 %, though the decrease was not statistically significant. Under normal conditions, MT had no considerable effect on proline levels.

MT lowers H_2O_2 build-up under salinity

Elevating hydrogen peroxide (H_2O_2) levels indicates plant exposure to stress conditions. The results revealed that salinity significantly ($P \leq 0.05$) increased H_2O_2 levels by 41.7 % compared to the control group (Fig. 8). Interestingly, MT supplementation under non-stress conditions doubled the H_2O_2 levels compared to the control. However, under salt stress, MT treatment significantly reduced H_2O_2 levels by 67.4 % ($P < 0.05$).

The effects of MT on antioxidant activities

The antioxidant enzyme system plays a critical role in plant salt tolerance. In this study, the activities of SOD, APX and CAT were measured to evaluate the effect of MT on enhancing cowpea's salt tolerance. The results revealed that salinity significantly increased SOD activity by 85.5 % compared with the control ($P < 0.05$). MT application further boosted SOD activity by 75.5 % under non-saline conditions, while under saline conditions, it caused a slight, non-significant increase of 8.3 % (Fig. 9A). APX activity showed a modest increase of 5.9 % under salinity compared to the control (Fig. 9B). MT treatment slightly increased APX activity by 5.2 % under non-saline conditions and 3.1 % under salinity compared to their respective controls. CAT activity, however, displayed a more pronounced response. Salinity significantly ($P \leq 0.05$) enhanced CAT activity by 63.7 % compared to the control treatment, while MT application under non-saline conditions boosted CAT activity by 95.2 % (Fig. 9C). Interestingly, MT treatment under salinity conditions significantly ($P \leq 0.05$) reduced CAT activity by 30.6 % compared to salt-stressed plants without MT.

Impact of MT on total phenolic compounds, flavonoids and glutathione levels

The effects of MT on total phenols, flavonoids and glutathione content-key non-enzymatic antioxidants-were examined to evaluate its role in enhancing antioxidant capacity and stress tolerance in cowpea plants. Total phenol levels slightly increased under salt stress by 8.3 % compared to the control (Fig. 10A) and MT treatment had no significant effect on total phenol accumulation under salinity. In contrast, total flavonoid levels significantly ($P \leq 0.05$) increased in salt-stressed plants by an average of 12.1 % (Fig. 10B). However, the MT application significantly reduced total flavonoid levels under salinity ($P \leq 0.05$). MT slightly reduced glutathione levels under control conditions but had a minimal effect on total glutathione levels when cowpea plants were grown under salinity (Fig. 10C).

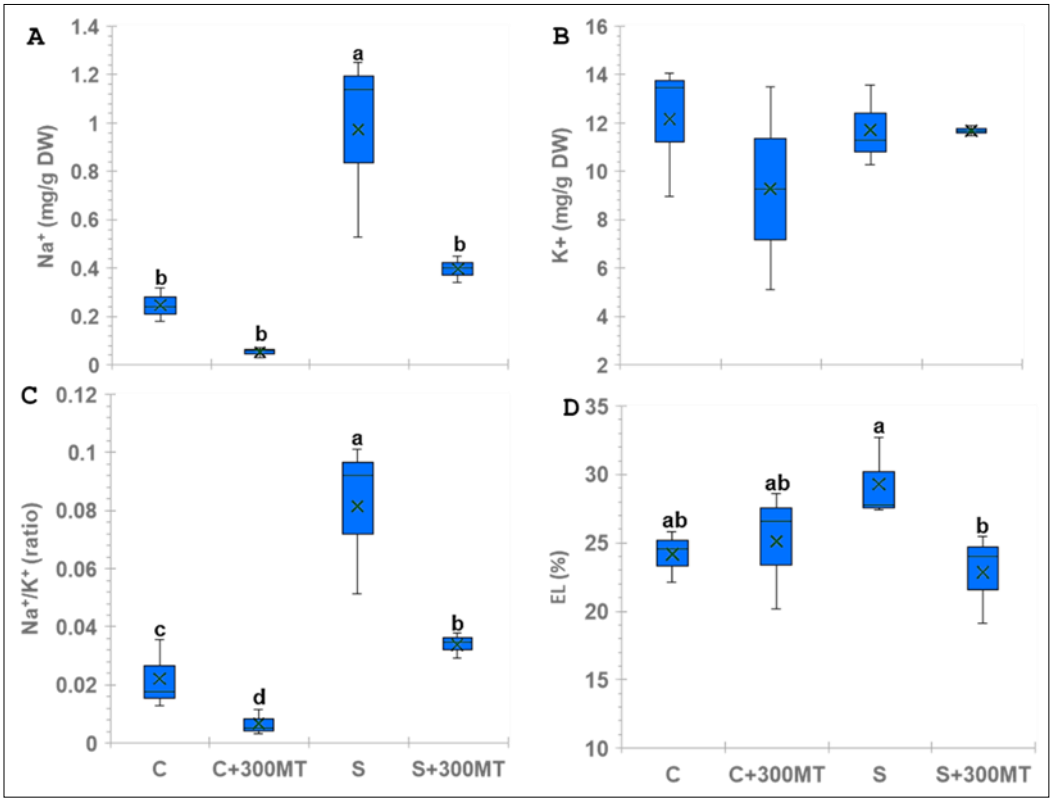

Fig. 6. The effect of 300 µM MT application on Na^+ concentration (A), K^+ concentration (B), Na^+/K^+ ratio (C) and the electrolyte leakage (EL) (D) in cowpea plants. Boxplots with different letters are significantly ($P \leq 0.05$) different, as evaluated by the LSD test.

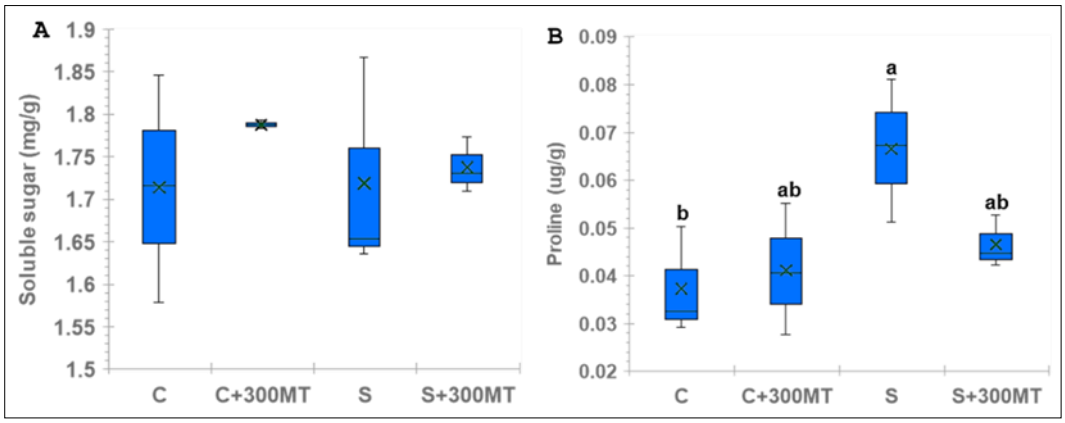

Fig. 7. Effect of salinity and MT treatment on soluble sugar (A) and proline contents (B) in cowpea plants. Boxplots with different letters are significantly ($P \leq 0.05$) different, as evaluated by the LSD test.

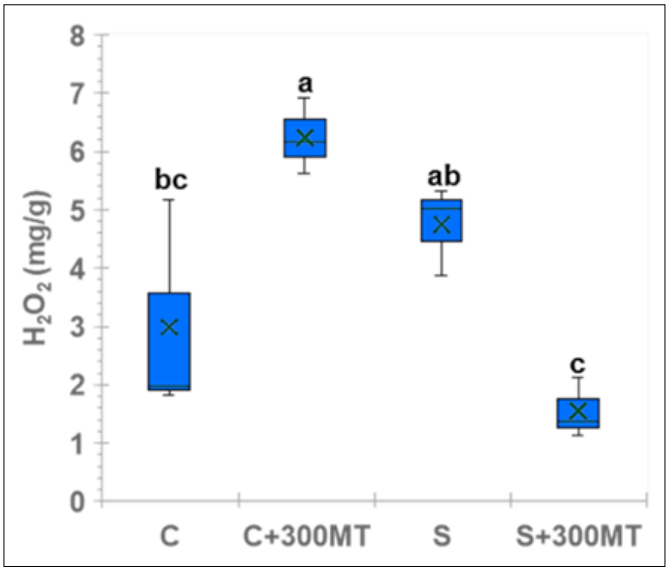

Fig. 8. Effect of salinity and MT treatment on H_2O_2 accumulation in the leaves of cowpea plants. Boxplots with different letters are significantly ($P \leq 0.05$) different, as evaluated by the LSD test

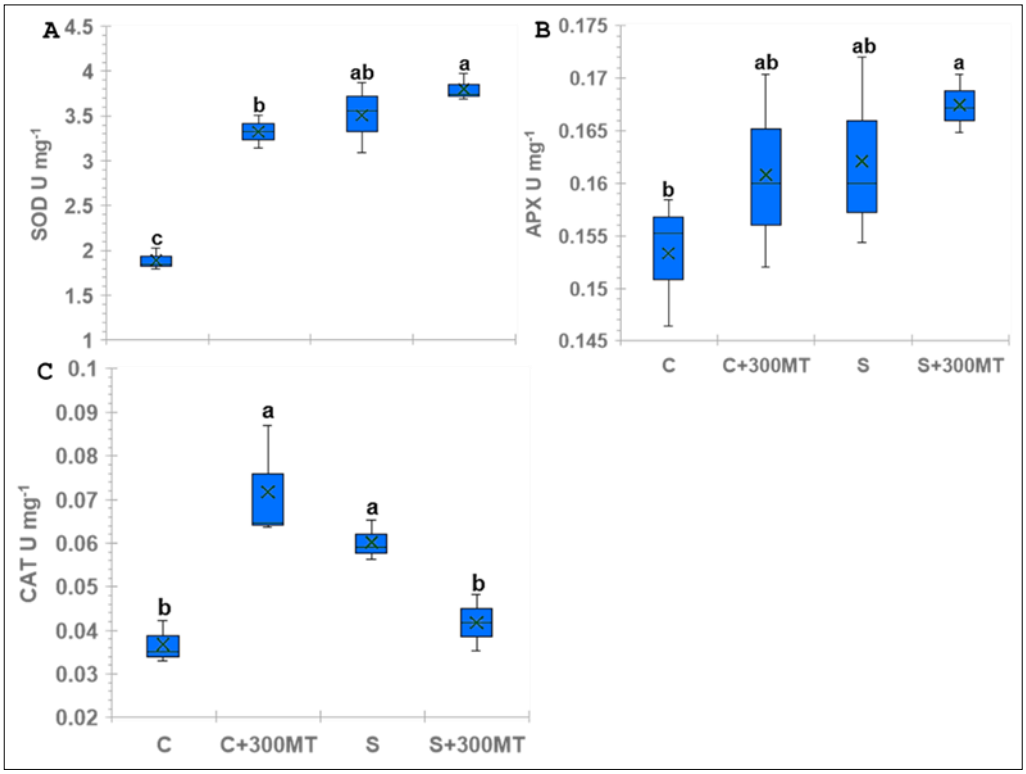

Fig. 9. Effect of salinity and MT treatment on SOD (A), APX (B) and CAT (C) enzymatic antioxidants in cowpea plants. Boxplots with different letters are significantly ($P \leq 0.05$) different, as evaluated by the LSD test.

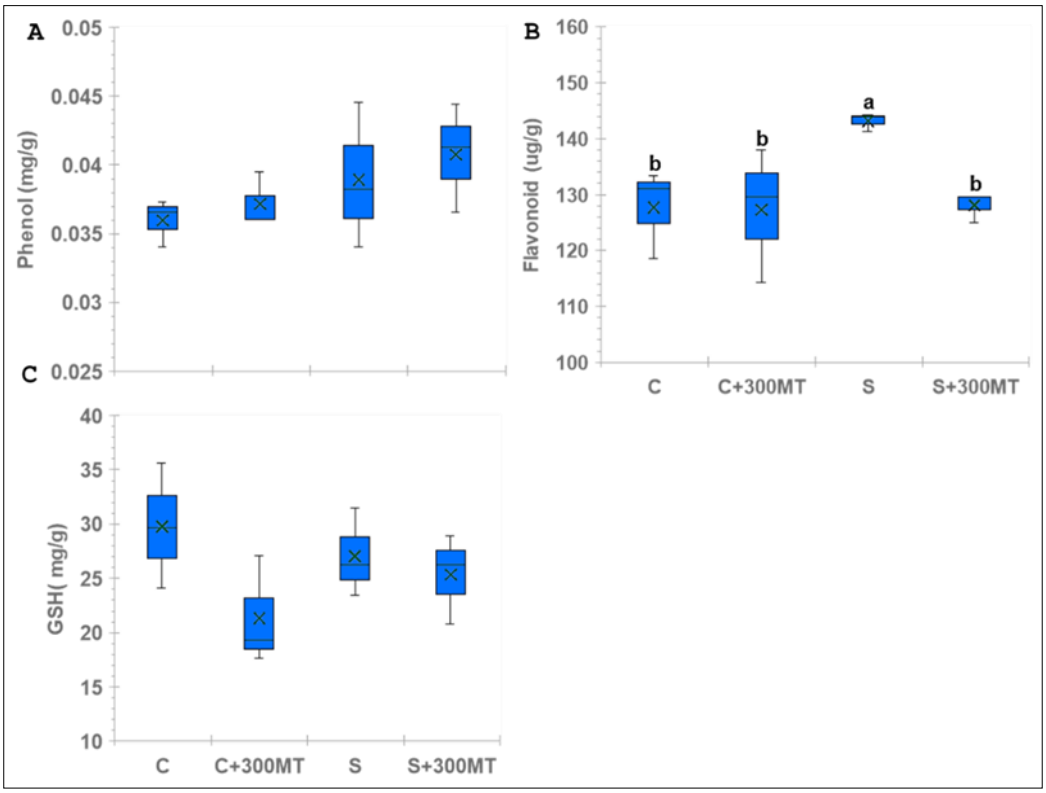

Fig. 10. Effect of salinity and MT treatment on phenol (A), flavonoid (B) and glutathione contents (C) in cowpea plants. Boxplots with different letters are significantly ($P \leq 0.05$) different, as evaluated by the LSD test.

Discussion

Our results consistently showed that salinity levels of 150 mM or higher could significantly impair cowpea growth. Selecting 150 mM NaCl as a salinity stressor is consistent with previous research, which has shown that this salinity level is a pre-lethal stage (11). A reduction in growth parameters, including plant height, fresh weight, dry weight, leaf area and root system parameters, can characterize this growth impairment. Additionally, various physiological and biochemical measurements were adversely affected by salinity. However, our findings showed that MT application enhances cowpea salinity tolerance by improving photosynthesis, antioxidant defense and ion balance, leading to increased growth and reduced oxidative damage (Fig. 11).

The MT enhancement effect was previously documented in other plant species, including cowpeas, when grown under drought

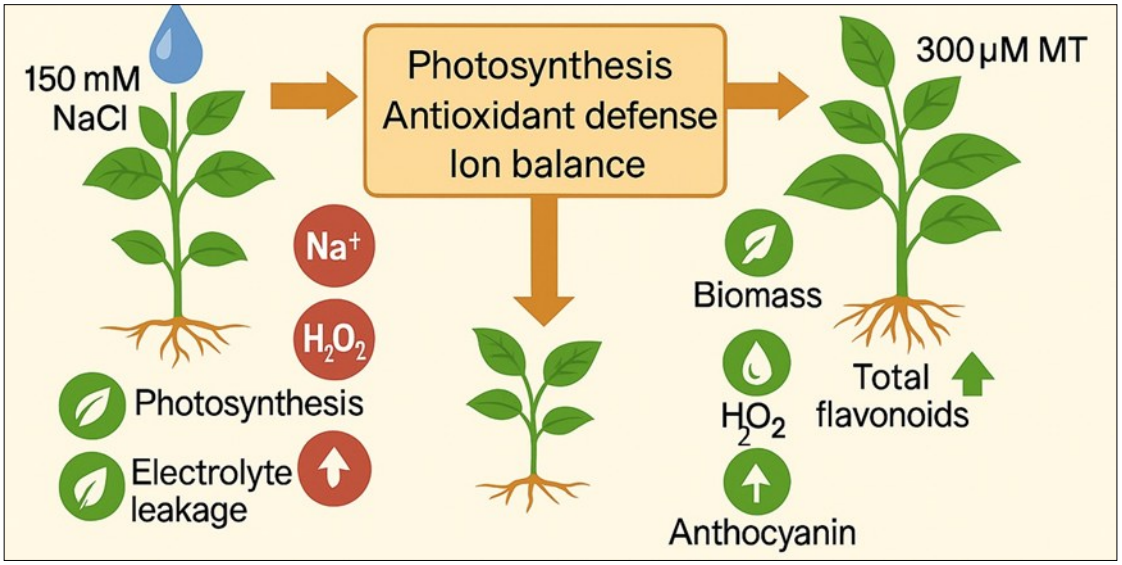

Fig. 11. A graphical abstract showing the effect of MT application on cowpeas' tolerance to salinity. The MT application enhances cowpea salinity tolerance by improving photosynthesis, antioxidant defense and ion balance, resulting in increased growth and reduced oxidative damage.

conditions and other crops such as green mustard, where MT improved plant height, leaf area and stem diameter and green beans, where MT increased the fresh and dry weight under salinity conditions (25-27).

Salt accumulation in the root zone increases osmotic stress, hindering water and nutrient uptake by roots and impeding cell division and elongation, thereby reducing root length and surface area (28). In our study, 150 mM NaCl significantly reduced root length, surface area and the number of root tips in cowpea seedlings, aligning with previous findings. However, our results indicated that applying MT can partially mitigate the adverse effects of salinity on cowpeas. This observation is supported by earlier research on other crops, which has shown that exogenous MT application under salinity increased root fresh and dry weight in pistachio and promoted the lateral roots development in cucumber (29, 30). This growth enhancement could previously be attributed to MT, which can modulate the form of action and may increase the level of indoleacetic acid (IAA) response in the plant roots (31).

Chlorosis or a reduction in chlorophyll content, is a symptom of salt stress resulting from the activation of the chlorophyllase enzyme and ion accumulation. Previous studies have shown that high salinity reduces chlorophyll and carotenoid concentrations in cowpeas, while moderate stress does not significantly affect photosynthetic pigmentation (32). Our findings indicated that the foliar application of MT enhanced anthocyanins, but other pigments were not significantly affected in the salt-stressed cowpeas. MT has previously induced anthocyanin accumulation in various plant species, including cabbage and red pear, likely because it differentially regulates the expression of genes involved in anthocyanin biosynthesis (33, 34). Previous studies have also shown that MT increases the chlorophyll and carotenoid content of strawberries under severe salt stress (35). Similarly, varying MT concentrations in green beans promote the concentration of chlorophyll and carotenoids under higher salt stress (36). This is likely because MT decreases chlorophyll and protein degradation, while also enhancing nitrogen and glucose metabolism, thereby alleviating photosynthetic limitations (37). However, this effect was not observed in the current study.

Salinity significantly affected all photosynthesis parameters assessed in this study. The results showed that *E*, *Gs*, *Ci* and *A* decreased; however, WUE increased due to salinity. Salt-stressed plants produce abscisic acid (ABA) as a stress hormone to enhance stomatal closure, thereby decreasing stomatal conductance and reducing CO_2 flux, which consequently reduces photosynthesis, transpiration and overall plant growth (38). A previous study on cowpeas reported a steady decrease in stomatal conductance and photosynthesis as the salt concentration increased (39). The increased WUE in cowpeas under saline stress is consistent with the drought and salinity-tolerant nature of cowpea plants and could be attributed to a greater reduction in transpiration rate and stomatal conductance than in the photosynthesis rate, thereby minimizing moisture loss (40).

Under saline conditions, MT application significantly enhanced *E*, *Gs* and *A*, indicating improved physiological performance of the cowpea plants. However, under non-saline control conditions, MT treatment significantly enhanced *E* and inhibited WUE, suggesting that its impact on plant water management, which ABA partially controls, may vary depending on the presence or absence of salt stress. This observation is consistent with a previous study in rice, which found that MT enhanced the *A*, *Gs* and *E* in salt-stressed rice but had no significant effect on *Ci* (41).

It is well known that salinity significantly affects the accumulation of Na^+ and K^+ in plants. Consistently, our findings demonstrated increased Na^+ accumulation with no significant effect on K^+ concentration in salt-stressed cowpeas. Notably, MT treatment effectively reduced Na^+ accumulation under saline conditions. Previous studies have reported variability in Na^+ and K^+ accumulation patterns among cowpea cultivars. For instance, one cultivar exhibited elevated K^+ levels and a favorable K^+/Na^+ ratio under high salinity conditions, while another exhibited high Na^+ accumulation and low K^+ levels under salt stress (42, 43). In addition to the genotype, the time of exposure and the age of the sampled tissue can give inconsistent results. For example, a lower level of K^+ concentration was detected in the first week, whereas K^+ levels were higher at a later growth stage of cowpeas (44). The observation recorded in this study that MT altered Na^+ but not K^+ levels, thereby affecting the Na^+/K^+ ratio, indicates that its protective effect in plants is likely mediated through Na-dependent mechanisms, potentially involving modulation of Na^+ transporters such as SOS1, NHX and HKT-type proteins that maintain ion homeostasis under stress.

Furthermore, the mechanism by which MT maintains the Na^+ concentration in plants under salinity is attributed to the induction of specific polyamine production, which is necessary for efficient ion exchange under salt stress (29).

Maintaining lower lipid peroxidation-induced membrane injury under salt stress, driven by ROS, reduces membrane damage and ion leakage a favorable trait for salt tolerance (6). The MT application decreased ion leakage (EL), in salt-stressed cowpea plants and in tomatoes and cucumbers, indicating that MT enhances salt tolerance by preserving membrane integrity and stability (45, 46).

Plants develop various salt tolerance strategies, including activating antioxidant enzymes such as APX, CAT and SOD to mitigate oxidative stress caused by abiotic stresses, such as salinity (6). In our study, SOD, CAT and APX activity were enhanced under salt stress. The foliar MT application slightly reduced SOD and APX activity, while significantly reducing CAT activity. This result may be attributed to decreased H_2O_2 accumulation in cowpeas following MT treatment, thereby reducing the cellular demand for elevated CAT activity.

MT increases plants' salt tolerance by enhancing antioxidant enzyme activity and reducing oxidative damage (36). Recently, it was discovered that there is crosstalk between the MT and ROS balance in plants under abiotic stress (47). However, MT treatment on plants under non-saline conditions may increase H_2O_2 levels by regulating ROS signaling pathways and stimulating metabolic processes, including respiration and photosynthesis, which can generate more H_2O_2 as byproducts.

This research did not show a significant increase in GSH, total phenols and flavonoid levels due to salinity; however, MT application significantly reduced flavonoid levels under saline conditions. Consistently, previous studies have shown that cowpeas exposed to salinity stress (up to 300 mM NaCl) exhibit a slight increase in leaf phenolic content, with no significant effect on flavonoid content (48). Salt-tolerant cowpeas exposed to salt stress demonstrated a non-significant decrease in GR activity after 14 days compared to the control, while salt-sensitive cowpeas showed an insignificant increase in GR activity (49). The MT application enhanced GSH in salt-stressed maize and cucumber (50, 51). However, MT has an insignificant effect on GSH content in salt-stressed rice, which may be attributed to variations in salt response mechanisms among different plant species (41). Different MT concentrations enhance the phenol and flavonoid content in salt-stressed cucumber compared to the salt control (51). In contrast, a previous study on green mustard showed that MT decreased total phenol and flavonoid content in salt-stressed seedlings (26).

Among the plant salt tolerance strategies is the accumulation of compatible osmolyte solutes, including proline and soluble sugars, which are water-soluble molecules that maintain cell turgor by reducing osmotic potential, allowing water molecules to enter the cell more efficiently (37). Proline and soluble sugars were enhanced under salinity in different cowpea cultivars (3). However, our results showed that salinity had no significant effect on soluble sugar accumulation in cowpeas, whereas proline levels increased significantly under salt stress. Additionally, MT treatment slightly reduced the proline content in salt-stressed cowpeas to levels similar to those of the control but did not affect soluble sugar content. Proline levels in cowpeas under salinity could be reduced by MT treatment, potentially through modulation of stress signaling pathways, enhancement of antioxidant system responses and alterations in metabolic pathways involved in proline synthesis and degradation (9).

The findings described in this study suggest that MT could be a promising biostimulant for improving cowpea productivity under saline conditions. Therefore, the study provided valuable insights into the positive effects of MT on enhancing plant tolerance to salinity. However, as the experiments were conducted under controlled environmental conditions using purified, analytical-grade MT, the results may differ under field environments where plants are exposed to variable salinity levels, complex soil microbiota and organic fertilizers that contain MT in less bioavailable forms. Moreover, ion concentrations in the roots and Cl^- accumulation were not measured, which limits a comprehensive understanding of the ionic adjustments and compartmentalization processes involved in MT-mediated salinity tolerance in cowpeas. Future studies should therefore include field trials and comprehensive ion profiling to validate these findings under agronomically relevant conditions.

Conclusion

MT significantly enhanced cowpea plants' salinity tolerance by improving photosynthetic performance, antioxidant defense and ion homeostasis. The key novelty of this work is that, for the first time in cowpeas, it reveals MT's role in enhancing salinity tolerance through these physiological and biochemical mechanisms. MT shows potential as a biostimulant to enhance cowpea productivity and salinity tolerance. However, field validation and further analysis of root ion dynamics, including Cl levels, are needed to fully elucidate its mechanism of action.

Acknowledgements

The authors thank the Department of Biology, College of Science, Sultan Qaboos University, for its generous support. This study was supported by the College of Science, Sultan Qaboos University, Oman, in the form of a grant awarded to MWY, IG/SCI/BIOL/24/03.

Authors' contributions

ISHAK was responsible for the writing of the original draft, as well as data curation, formal analysis, visualization and investigation. HEA contributed through supervision, data curation and by providing review and editing support. MWY took the lead in conceptualization and funding acquisition, while also overseeing supervision, project administration, methodology development and contributing to the review and editing process. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

AI Declaration: During the preparation of this work, the author(s) used [Open AI, ChatGPT and Grammarly] to only improve the readability and language of the work. The graphical abstract was

initially made with the help of the Consensus AI tool. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the published article.

References

1. Khattab HI, Sadak MS, Dawood MG, Elkady FM, Helal NM. Foliar application of esculin and digitoxin improve the yield quality of salt-stressed *Linum usitatissimum* by improving the antioxidant defense system. BMC Plant Biol. 2024;24(1):963. https://doi.org/10.1186/s12870-024-05626-z
2. Abebe BK, Alemayehu MT. A review of the nutritional use of cowpea (*Vigna unguiculata* L. Walp) for human and animal diets. J Agric Food Res. 2022;10:100383. https://doi.org/10.1016/j.jafr.2022.100383
3. Mini M, Sathya M, Arulvadivookarasi K, Jayachandran K, Anusuyadevi M. Selection of salt tolerant cowpea genotypes based on salt tolerant indices of morpho-biochemical traits. Curr Trends Biotechnol Pharm. 2015;9:306-16.
4. Zhou H, Shi H, Yang Y, Feng X, Chen X, Xiao F, et al. Insights into plant salt stress signalling and tolerance. J Genet Genomics. 2024;51(1):16-34. https://doi.org/10.1016/j.jgg.2023.08.007
5. Hu Y, Wang D, Zhang X, Lv X, Li B. Current progress in deciphering the molecular mechanisms underlying plant salt tolerance. Curr Opin Plant Biol. 2025;83:102671. https://doi.org/10.1016/j.pbi.2024.102671
6. Jiang L, Xiao M, Huang R, Wang J. The regulation of ROS and phytohormones in balancing crop yield and salt tolerance. Antioxidants. 2025;14(1):63. https://doi.org/10.3390/antiox14010063
7. Al Kharusi L, Al Yahyai R, Yaish MW. Antioxidant response to salinity in salt-tolerant and salt-susceptible cultivars of date palm. Agriculture. 2019;9(1):8. https://doi.org/10.3390/agriculture9010008
8. Sadak MS, Ramadan AAE-M. Impact of melatonin and tryptophan on water stress tolerance in white lupine (*Lupinus termis* L.). Physiol Mol Biol Plants. 2021;27(3):469-81. https://doi.org/10.1007/s12298-021-00958-8
9. Faizan M, Sultan H, Alam P, Karabulut F, Cheng S-H, Rajput VD, et al. Melatonin and its cross-talk with other signalling molecules under abiotic stress. Plant Stress. 2024;11:100410. https://doi.org/10.1016/j.stress.2024.100410
10. Arnao MB, Hernández-Ruiz J. Melatonin as a chemical substance or as phytomelatonin-rich extracts for use as plant protector and/or biostimulant in accordance with EC legislation. Agronomy. 2019;9(10):570. https://doi.org/10.3390/agronomy9100570
11. Rajendra F, Kristiani L, Ariviani S, editors. Elicitation under salinity stress increases flavonoid content and antioxidant activity in cowpea (*Vigna unguiculata*) sprouts. In: IOP Conference Series: Materials Science and Engineering; 2019: IOP Publishing. https://doi.org/10.1088/1757-899X/633/1/012034
12. Porra RJ, Thompson WA, Kriedemann PE. Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls a and b extracted with four different solvents: Verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. Biochim Biophys Acta (BBA)-Bioenergetics. 1989;975(3):384-94. https://doi.org/10.1016/S0005-2728(89)80347-0
13. Munns R, Wallace PA, Teakle NL, Colmer TD. Measuring soluble ion concentrations (Na^+, K^+, Cl^-) in salt-treated plants. In: Methods in Molecular Biology. Humana Press; 2010. p. 371-82. https://doi.org/10.1007/978-1-60761-702-0_23
14. Assaha DV, Liu L, Ueda A, Nagaoka T, Saneoka H. Effects of drought stress on growth, solute accumulation and membrane stability of leafy vegetable, huckleberry (*Solanum scabrum* Mill.). J Environ Biol. 2016;37(1):107-14.
15. Alexieva V, Sergiev I, Mapelli S, Karanov E. The effect of drought and ultraviolet radiation on growth and stress markers in pea and wheat. Plant Cell Environ. 2001;24(12):1337-44. https://doi.org/10.1046/j.1365-3040.2001.00778.x
16. Yan F, Wei H, Ding Y, Li W, Liu Z, Chen L, et al. Melatonin regulates antioxidant strategy in response to continuous salt stress in rice seedlings. Plant Physiol Biochem. 2021;165:239-50. https://doi.org/10.1016/j.plaphy.2021.06.031
17. Nakano Y, Asada K. Hydrogen peroxide is scavenged by ascorbate-specific peroxidase in spinach chloroplasts. Plant Cell Physiol. 1981;22(5):867-80. https://doi.org/10.1093/oxfordjournals.pcp.a076232
18. Wieland T, Pfleiderer G. Isozymes and heteroenzymes. Angew Chem Int Ed Engl. 1962;1(4):169-78.
19. Beauchamp C, Fridovich I. Superoxide dismutase: improved assays and an assay applicable to acrylamide gels. Anal Biochem. 1971;44(1):276-87.
20. Ahmad S, Cui W, Kamran M, Ahmad I, Meng X, Wu X, et al. Exogenous application of melatonin induces tolerance to salt stress by improving the photosynthetic efficiency and antioxidant defense system of maize seedling. J Plant Growth Regul. 2020;40(3):1270-83. https://doi.org/10.1007/s00344-020-10245-2
21. Lamaison J, Carant A. The amount of main flavonoids in flowers and leaves of *Crataegus monogyna* Jacq. and *Crataegus laevigata* (Poir.) DC. (*Rosacea*). Pharm Acta Helv. 1996;65:315-20.
22. Singleton VL, Orthofer R, Lamuela-Raventós RM. Analysis of total phenols and other oxidation substrates and antioxidants by means of Folin-Ciocalteu reagent. In: Methods in Enzymology. 1999;299:152-78.
23. Loewus MW, Briggs D. The number of catalytically active sites present on the chymotrypsin molecule. J Biol Chem. 1952;199(2):857-64.
24. Bates LS, Waldren R, Teare I. Rapid determination of free proline for water-stress studies. Plant Soil. 1973;39:205-7. https://doi.org/10.1007/BF00018060
25. Al Khatri ISH, Ali HE, Yaish M. Melatonin improves drought tolerance in cowpea through growth modulation, antioxidant response and ionic homeostasis, supporting sustainable agriculture. Environ Res Commun. 2025;7:055019. https://doi.org/10.1088/2515-7620/add85f
26. Park H-S, Kazerooni EA, Kang S-M, Al-Sadi AM, Lee I-J. Melatonin enhances the tolerance and recovery mechanisms in *Brassica juncea* (L.) Czern. under saline conditions. Front Plant Sci. 2021;12:593717. https://doi.org/10.3389/fpls.2021.593717
27. ElSayed AI, Rafudeen MS, Gomaa AM, Hasanuzzaman M. Exogenous melatonin enhances the reactive oxygen species metabolism, antioxidant defense-related gene expression and photosynthetic capacity of *Phaseolus vulgaris* L. to confer salt stress tolerance. Physiol Plant. 2021;173(4):1369-81. https://doi.org/10.1111/ppl.13385
28. Sadak MS, Dawood MG. Biofertilizer role in alleviating the deleterious effects of salinity on wheat growth and productivity. Gesunde Pflanzen. 2023;75(4):1207-19. https://doi.org/10.1007/s10343-022-00653-4
29. Kamiab F. Exogenous melatonin mitigates the salinity damages and improves the growth of pistachio (*Pistacia vera*) under salinity stress. J Plant Nutr. 2020;43(10):1468-84. https://doi.org/10.1080/01904167.2019.1627353
30. Zhang N, Zhao B, Zhang H J, Weeda S, Yang C, Yang Z C, et al. Melatonin promotes water-stress tolerance, lateral root formation and seed germination in cucumber (*Cucumis sativus* L.). J Pineal Res. 2013;54(1):15-29. https://doi.org/10.1111/jpi.12018
31. Adil M, Abbasi BH, Khan T. Interactive effects of melatonin and light on growth parameters and biochemical markers in adventitious roots of *Withania somnifera* L. Plant Cell Tissue Organ Cult. 2015;123:405-12. https://doi.org/10.1007/s11240-015-0834-1
32. El-Taher AM, El-Raouf A, Hany S, Osman NA, Azoz SN, Omar MA, et al. Effect of salt stress and foliar application of salicylic acid on morphological, biochemical, anatomical and productivity characteristics of cowpea (*Vigna unguiculata* L.) plants. Plants. 2022;11(1):115. https://doi.org/10.3390/plants11010115

33. Zhang N, Sun Q, Li H, Li X, Cao Y, Zhang H, et al. Melatonin improved anthocyanin accumulation by regulating gene expressions and resulted in high reactive oxygen species scavenging capacity in cabbage. Front Plant Sci. 2016;7:197. https://doi.org/10.3389/fpls.2016.00197

34. Sun H, Cao X, Wang X, Zhang W, Li W, Wang X, et al. RBOH-dependent hydrogen peroxide signalling mediates melatonin-induced anthocyanin biosynthesis in red pear fruit. Plant Sci. 2021;313:111093. https://doi.org/10.1016/j.plantsci.2021.111093

35. Zahedi SM, Hosseini MS, Fahadi Hoveizeh N, Gholami R, Abdelrahman M, Tran LSP. Exogenous melatonin mitigates salinity-induced damage in olive seedlings by modulating ion homeostasis, antioxidant defense and phytohormone balance. Physiol Plant. 2021;173(4):1682-94. https://doi.org/10.1111/ppl.13398

36. Azizi F, Amiri H, Ismaili A. Melatonin improves salinity stress tolerance of *Phaseolus vulgaris* L. cv. Pak by changing antioxidant enzymes and photosynthetic parameters. Acta Physiol Plant. 2022;44(4):40. https://doi.org/10.1007/s11738-022-03106-w

37. Siddiqui MH, Alamri S, Al-Khaishany MY, Khan MN, Al-Amri A, Ali HM, et al. Exogenous melatonin counteracts NaCl-induced damage by regulating the antioxidant system, proline and carbohydrates metabolism in tomato seedlings. Int J Mol Sci. 2019;20(2):353. https://doi.org/10.3390/ijms20020353

38. Ouerghi Z, Cornic G, Roudani M, Ayadi A, Brulfert J. Effect of NaCl on photosynthesis of two wheat species (*Triticum durum* and *T. aestivum*) differing in their sensitivity to salt stress. J Plant Physiol. 2000;156(3):335-40. https://doi.org/10.1016/S0176-1617(00)80071-1

39. Wilson C, Liu X, Lesch SM, Suarez DL. Growth response of major USA cowpea cultivars: II. Effect of salinity on leaf gas exchange. Plant Sci. 2006;170(6):1095-101. https://doi.org/10.1016/j.plantsci.2006.03.029

40. Abbas K, Li J, Gong B, Lu Y, Wu X, Lü G, et al. Drought stress tolerance in vegetables: the functional role of structural features, key gene pathways and exogenous hormones. Int J Mol Sci. 2023;24(18):13876. https://doi.org/10.3390/ijms241813876

41. Yan F, Zhang J, Li W, Ding Y, Zhong Q, Xu X, et al. Exogenous melatonin alleviates salt stress by improving leaf photosynthesis in rice seedlings. Plant Physiol Biochem. 2021;163:367-75. https://doi.org/10.1016/j.plaphy.2021.05.016

42. Taffouo VD, Kouamou JK, Ngalangue LT, Ndjeudji BAN, Akoa A. Effects of salinity stress on growth, ions partitioning and yield of some cowpea (*Vigna unguiculata* L. Walp.) cultivars. Int J Bot. 2009;5(2):135-43. 10.3923/ijb.2009.135.143

43. Salih HO, Kia DR. Effect of salinity level of irrigation water on cowpea (*Vigna unguiculata*) growth. J Agric Veter Sci. 2013;6(3):37-41.

44. Lacerda CF, Assis Júnior JO, Lemos Filho LC, Oliveira TSd, Guimarães FV, Gomes-Filho E, et al. Morpho-physiological responses of cowpea leaves to salt stress. Braz J Plant Physiol. 2006;18:455-65. https://doi.org/10.1590/S1677-04202006000400007

45. Ali M, Kamran M, Abbasi GH, Saleem MH, Ahmad S, Parveen A, et al. Melatonin-induced salinity tolerance by ameliorating osmotic and oxidative stress in the seedlings of two tomato (*Solanum lycopersicum* L.) cultivars. J Plant Growth Regul. 2021;40:2236-48. https://doi.org/10.1007/s00344-021-10384-2

46. Wang L, Liu J, Wang W, Sun Y. Exogenous melatonin improves growth and photosynthetic capacity of cucumber under salinity-induced stress. Photosynthetica. 2016;54:19-27. https://doi.org/10.1007/s11099-015-0199-7

47. Zhao J, Hu J. Melatonin: current status and future perspectives in horticultural plants. Front Plant Sci. 2023;14:1140803. https://doi.org/10.3389/fpls.2023.1140803

48. Jayawardhane J, Goyali JC, Zafari S, Igamberdiev AU. The response of cowpea (*Vigna unguiculata*) plants to three abiotic stresses applied with increasing intensity: hypoxia, salinity and water deficit. Metabolites. 2022;12(1):38. https://doi.org/10.3390/metabo12010038

49. Praxedes SC, Damatta FM, Lacerda CF, Prisco JT, Gomes-Filho E. Salt stress tolerance in cowpea is poorly related to the ability to cope with oxidative stress. Acta Bot Croat. 2014;73(1):51-62. https://doi.org/10.3989/abot.37313

50. Chen YE, Mao JJ, Sun LQ, Huang B, Ding CB, Gu Y, et al. Exogenous melatonin enhances salt stress tolerance in maize seedlings by improving antioxidant and photosynthetic capacity. Physiol Plant. 2018;164(3):349-63. https://doi.org/10.1111/ppl.12773

51. Liu T, Xing G, Chen Z, Zhai X, Wei X, Wang C, et al. Effect of exogenous melatonin on salt stress in cucumber: alleviating effect and molecular basis. Biotechnol Biotechnol Equip. 2022;36(1):818-27. https://doi.org/10.1080/13102818.2022.2105581

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etcSee https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.