

N-acetyl-5-methoxytryptamine as an enhancer of salinity tolerance via modulating physiological and anatomical attributes in faba bean

Ramadan K.M.A.¹, Mohamed H.A.², Al Hashedi S.A.¹, Ghazzawy H.S.², El-Beltagi H.S.^{3*}, El-Mogy M.M.⁴, Mohamed M.S.⁵, Saudy H.S.^{6*}, Abdelkhalik A.⁷, Abd El-Mageed S.A.⁵, Mohamed I.A.A.⁸ and Abd El-Mageed T.A.⁹

¹Central Laboratories, Department of Chemistry, King Faisal University, Al-Ahsa 31982, Saudi Arabia

²Date Palm Research Center of Excellence, King Faisal University, P.O. Box 400, Al-Ahsa 31982, Saudi Arabia

³Agricultural Biotechnology Department, College of Agriculture and Food Sciences, King Faisal University, Al-Ahsa 31982, Saudi Arabia

⁴Department of Arid Land Agriculture, College of Agricultural and Food Sciences, King Faisal University, Al-Ahsa 31982, Saudi Arabia

⁵Agronomy Department, Faculty of Agriculture, Fayoum University, Fayoum 63514, Egypt

⁶Agronomy Department, Faculty of Agriculture, Ain Shams University, 68-Hadayek Shoubra 11241, Cairo, Egypt

⁷Horticulture Department, Faculty of Agriculture, Fayoum University, Fayoum 63514, Egypt

⁸Botany Department, Faculty of Agriculture, Fayoum University, Fayoum 63514, Egypt

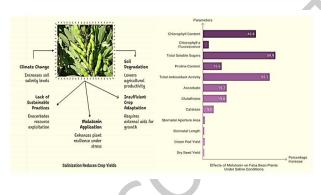
⁹Soil and Water Department, Faculty of Agriculture, Fayoum University, 63514, Fayoum, Egypt

Received: 02/04/2025, Accepted: 29/04/2025, Available online: 29/04/2025

*to whom all correspondence should be addressed: e-mail: helbeltagi@kfu.edu.sa, hani_saudy@agr.asu.edu.eg

https://doi.org/10.30955/gnj.07515

Graphical abstract



Abstract

To meet the increasingly food demands, all environmental resources should be exploited in sustainable manner. Soil, a major component in agricultural for production, is subjected to salinization owing to climate changes. Growing crop plants in saline soil dramatically results in significant yield declines. Hence, crops require external aids to obtain rational quantity and quality of the economic product while achieving the land sustainability. Accordingly, a two-year field experiment was implemented for outstanding the probable changes in physiology and anatomy occurring in melatonin-treated faba bean plants under saline conditions. In randomized complete block design with three replicates, three levels of melatonin (0, 50 and 100 µM) were tested under salty stress conditions. The result data illustrated that application of melatonin (50 or 100 µM) maintained cell membrane stability index and

leaf water content of salt-suffered faba bean plants. Chlorophyll content, chlorophyll a fluorescence, total soluble sugars, proline content, total antioxidant activity, ascorbate, glutathione and catalase were increased by 43.8, 5.0, 59.9, 15.6, 55.1, 19.7, 19.6, and 9.0%, respectively, owing to melatonin (100 μ M) supply. Remarkable increases in stomatal aperture area and stomatal length were obtained with spraying of melatonin. Also, melatonin-treated faba bean plants at a rate of 100 μ M showed increases of 1.75 and 1.33 folds in green pod yield and dry seed yield greater than the salt-suffered plants. In conclusion, regulation of faba bean plant growth can be adjusted in favour of a healthy physiological status and sustainable productivity under saline soils using melatonin at a rate of 100 μ M.

Keywords: Lipid peroxidation, osmo-protectants, osmotic pressure, photosynthetic efficiency, physiological stress, stomatal conductivity, vicia faba

1. Introduction

Soil salinization is expected to increase over time owing to the possible climatic changes. It is well known that stresses of different types represent a drastic impediment in agricultural production (Saudy *et al.*, 2021; Ansabayeva *et al.* 2025; Emam *et al.*, 2025). Growth and yield of most crops are dramatically depressed by biotic and abiotic stresses such as pests, extreme temperatures, drought, salinity, and nutrient deficiency (Saudy *et al.*, 2022; Abou El-Enin *et al.*, 2023; Ramadan *et al.*, 2023a; Abdo *et al.*, 2024). Such various stresses stimulate the excess formation of free radicals within plant cells, mainly expressed in

Ramadan K.M.A., Mohamed H.A., Al Hashedi S.A., Ghazzawy H.S., El-Beltagi H.S., El-Mogy M.M., Mohamed M.S., Saudy H.S., Abdelkhalik A., Abd El-Mageed S.A., Mohamed I.A.A. and Abd El-Mageed T.A. (2025), N-acetyl-5-methoxytryptamine as an enhancer of salinity tolerance via modulating physiological and anatomical attributes in faba bean, *Global NEST Journal*, **27**(XX), 1-10.

reactive oxygen species (ROS), particularly, superoxide radical (O₂^{•-}), singlet oxygen (1O₂), hydroxyl radical (•OH) and hydrogen peroxide (H₂O₂), which are highly vulnerable and dramatically disturb plant metabolism while causing serious negative impacts on crop productivity (El-Beltagi et al., 2022 a; Abd El-Mageed et al., 2022; Hadid et al., 2023). Additionally, osmotic stress and toxicity of ions are the two major hazardous impacts of salinity (Van Zelm and Testerink, 2020; Selvanarayanan et al, 2024). Accordingly, salt stress is associated with alteration in the expression of genes, stability of mRNA, and translational regulation, disturbing proteins synthesis (Sharma and Dietz, 2009; Yashodha et al., 2025). It has been documented that these stress agents influence normal plant growth and development, resulting in lower yield outcomes with poor quality (Shabbir et al., 2022). In faba bean (Vicia faba, L.), such stresses have significantly negative impacts on growth, yield and quality, threatening food security (Saudy et al., 2020; El-Bially et al., 2023). In order to adapt to stresses, plants have evolved intricate mechanisms involving enzymatic and non-enzymatic antioxidant defines to maintain ROS within plant cells at a harmless level (Sharma et al., 2019; Ramadan et al., 2023). Furthermore, a variety of hormonal activities had a substantial action in regulation the adaptive response of plants to the stresses (El-Beltagi et al., 2022b; Rizk et al., 2023).

Recently, melatonin has exhibited as a powerful and dynamic regulator of abiotic stress tolerance in plant biology (Pan et al., 2023; El-Beltagi et al., 2023). Melatonin is regarded as a significant molecule in a diverse plant physiological process, such as germination of seeds, root development, movement of stomata and different responses to stresses (Pan et al., 2023; Jensen et al., 2023). Melatonin acts as a signalling molecule, controlling the growth and development of plants as well as the responses to ecological pressures (Altaf et al., 2021). Melatonin acts in harmony with other phytohormones. Substantial relations between melatonin and various related-stresses plant hormones such as salicylic acid, indole acetic acid, ethylene, cytokines and abscisic acids have been documented (Wang et al., 2022; Yang et al., 2021; Yang et al., 2022). Based on the physiological aspects, melatonin has the potential to affect salinity tolerance; however, the

changes in plant anatomy due to melatonin supply under salt stress did not sufficiently investigate. The current work hypothesized that melatonin could enhance the physiological status of faba bean plant while modifying anatomical appearance of leaf. Therefore, the current work aimed to assess the potential action of three levels of melatonin the physiological and anatomical traits of faba bean grown in saline soil.



Figure 1. Faba bean cultivation timeline

2. Materials and methods

2.1. Experimental site description

Two field trials were conducted over two succeeding seasons (2022/23 and 2023/24) at a private field (latitudes 29°06' and 29°35' N, longitudes 30°26' and 31°05' E.), in Fayoum province of Egypt. Primary physio-chemical properties of the investigated soil were measured in accordance with (Klute and Dirksen, 1986) and (Page *et al.*, 1982) and data were presented in **Table 1**.

Table 1. Some initial physico- chemical characteristics of the studied soils

Particle size (%)		Texture class	Bd (g cm ⁻³⁾	ECe (dS m ⁻¹)	рН	OM (%)	CaCO₃ (%)	CEC (cmol kg ⁻¹)	
Sand	Sil	Clay	_						
75.2	11.7	13.1	LS	1.56	7.83	7.61	1.02	4.47	10.25

LS: loamy sand Bd: soil bulk density, ECe: electrical conductivity, pH: soil acidity, OM: organic matter content, CaCO3: calcium carbonate, CEC: cation exchange capacity

2.2. Agronomic management and treatments

Healthy seeds of faba bean, (*Vicia faba* L.) cv. Sakha 1, were sown on November 1 and 5 and harvested on March 26 and 31 for two winter consecutive seasons 2022/23 and 2023/24, respectively. Melatonin was used to spray plant foliage at three concentrations (0; tap water as a control, 50 and 100 μ M) three times 15 days intervals beginning

from 20 days after sowing (DAS) to run-off. Tween-20 (0.1%, v/v), as a surfactant agent, was compiled with the sprays to ensure optimal penetration into leaf tissues (**Figure 1**).

The three tested melatonin concentrations were replicated three times in a random complete block design, totalling 9 experimental plots. Each experimental plot had a 36.0 m2 net area with three planting ridges and 0.8 m width and 15 m length. Faba bean seeds were sown in hills spaced 20 cm apart on two sides of the planting ridge, and seedlings

thinned to two healthy and uniform plants per hill four weeks after planting. Phosphorus (P) fertilizer with a rate of 75 kg P ha⁻¹ in the form of calcium superphosphate (15.5% P_2O_5) was basically added at planting and potassium (K) fertilizer with a rate of 120 kg K ha⁻¹ in the form of potassium sulfate (48% K₂O) was topdressed at four weeks after planting. Nitrogen (N) fertilizer was added once as a starter dose 10 DAS with a rate of 48 kg N ha⁻¹ in the form of ammonium nitrate (33.5% N). A drip irrigation system was sited, and two drip lines were placed 25 cm apart in every elementary test plot.

2.3. Cell membrane stability and leaf water

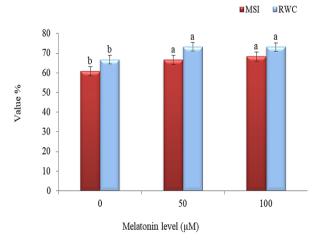
At 75 DAS, relative water content (RWC %) and membrane stability index (MSI %) were assessed according to (Hayat *et al.,* 2007) and (Premachandra *et al.,* 1990), respectively.

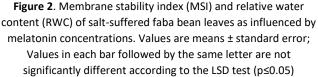
2.4. Leaf photosynthetic traits

Leaf chlorophyll content was extracted and determined (in mg g⁻¹ fresh weight; FW) according to the procedure of (Arnon, 1949). Chlorophyll a fluorescence (Fv/Fm) and performance index were determined according to (Maxwell and Johnson, 2000) and (Clark *et al.,* 2000) by Handy PEA, Hansatech Instruments (Ltd, Kings Lynn, UK).

2.5. Osmolytes and antioxidants

The free proline content and total soluble sugars (TSS) (mg g^{-1} FW) of fresh faba bean leaves were extracted and quantified using the procedures described by (Irigoyen *et al.*, 1992). The 2, 2-diphenyl-1-picrylhydrazyl (DPPH) radical-scavenging activity (DPPH RSA %) of the extract was calculated by DPPH free radical according to (Brand-Williams *et al.*, 1995). The ascorbic acid (AsA; µmol g^{-1} FW) and reduced glutathione (GSH; µmol g^{-1} FW) contents in fresh leaf tissues of faba bean were determined using the techniques outlined by Mukherjee and Choudhuri (Mukherjee and Choudhuri, 1983). Plant cells were extracted following the technique of (Bradford, 1976) for use as a crude enzyme extract to measure CAT content (U mg⁻¹ protein). CAT activity was established using the approach published by (Aebi, 1984).





2.6. Stomatal performance

To estimate the guard cell dimensions, stomatal apertures area, and stomatal density measurements, for this purpose, three plants per replicate (3 replicates for each treatment; total 9 plants) were selected. The measurements were performed for one well expanded leaf (on 6th node from the shoot apex) of each plant. From lower surface, the sample of epidermal cells was obtained (abaxial side) by nail varnish technique (Agami et al., 2016). A small area of abaxial then was observed through a light microscope (BX60, Olympus, Hamburg, Germany), equipped with a digital camera (Camedia C4040, Olympus, Hamburg, Germany). Stomata dimensions, stomatal aperture area, and stomata density were assessment with the software of AnalySIS®3.2 program for image analysis (Olympus, Hamburg, Germany) and their frequency (n/mm^2) .

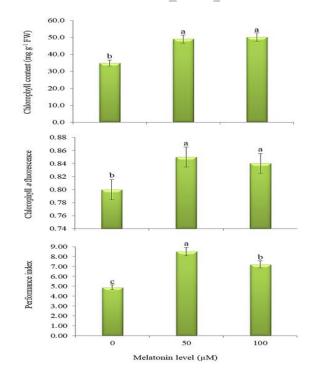


Figure 3. Chlorophyll content (mg g-1 fresh weight), chlorophyll a fluorescence and performance index of salt-suffered faba bean as influenced by melatonin concentrations. FW: fresh weight. Values are means ± standard error; Values in each bar followed by the same letter are not significantly different according to the

LSD test (p≤0.05)

2.7. Agronomic attributes

At 90 DAS, ten plants were randomly obtained from every experimental plot and assessed for their growth characteristics. First, plant height was recorded and then branches plant⁻¹ were counted. Next, the total leaf area plant⁻¹ was measured using a digital plan meter Planix 7 (Sokkia Co., Ltd. Kanagawa, Japan). The plant leaves and branches were dried in oven at 70 °C until constant weight then the plant dry weight was recorded. Once faba bean pods attained commercial green maturation for fresh pod human consumption, all green pods from all plants in one planting ridge from each experimental plot were handharvested, and the obtained value was then converted to a hectare basis (t ha⁻¹). At the harvesting stage (full maturation) of dry pods, 10 plants randomly were selected from each experimental plot and used to determine yield components, i.e., number of pods per plant and seed index. The faba bean dry seed yield on a 13% seed moisture basis was appreciated after the threshing of the dried plants harvested from the remaining two planting ridges in each plot.

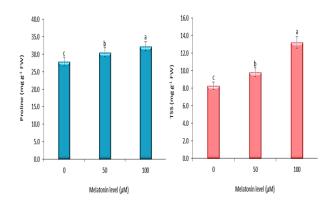
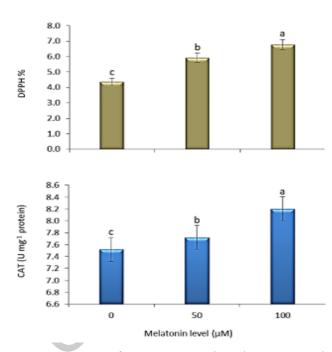


Figure 4. Proline and total soluble sugars (TSS) of salt-suffered faba bean as influenced by melatonin concentrations. FW: fresh weight. Values are means ± standard error; Values in each bar followed by the same letter are not significantly different according to the LSD test (p≤0.05)



2.8. Statistical analysis

Data were statistically examined following (Gomez and Gomez, 1984) with a two-way analysis of variance using the general linear model (GLM) procedure of GenStat statistical package (version 11) (VSN International Ltd, Oxford, UK) to test significant differences among treatments. While replications were regarded as a random factor, the three tested Me-applied concentrations were considered a fixed factor. When the F-value was significant ($p \le 0.05$), significant differences among treatments for each attribute were investigated using Fisher's protected LSD test.

3. Results

3.1. Cell membrane stability and leaf water

Different melatonin levels had substantial effects (p<0.05) on cell membrane stability index and leaf water content of faba bean plants grown in saline soil (**Figure 2**). Application of melatonin at a rate of 50 or 100 μ M surpassed the control treatment (without melatonin supply) for maintaining cell membrane stability index and leaf water content. The improvements were 9.5 and 12.4% in cell membrane stability and 9.8 and 9.6 in leaf water content with supplying 50 and 100 μ M, respectively. The differences between 50 and 100 μ M treatments were not significant (p>0.05) in this respect.

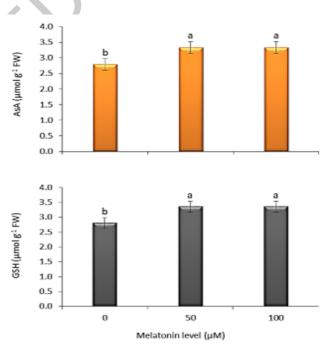


Figure 5. The activity of total antioxidants (DPPH), ascorbate AsA), catalase (CAT) and glutathione (GSH) of salt-suffered faba bean as influenced by melatonin concentrations. FW: fresh weight. Values are means \pm standard error; Values in each bar followed by the same letter are not significantly different according to the LSD test (p \leq 0.05)

Table 2. Stomatal performance traits of salt-suffered faba bean as influenced by melatonin concentrations

Melatonin level (µM)	Stomata aperture area (µ²)	Stomata density (no. mm ⁻¹)	Stomata length (μ)	Stomata width (μ)
0	162.30±10.79b	8.36±0.35a	40.72±1.02c	26.72±0.60a
50	185.40±7.10ab	7.67±0.36a	43.22±0.58b	27.96±0.72a
100	212.70±13.6a	7.34±0.26a	45.07±0.63a	28.80±0.58a

Values are means \pm standard error; Values in each column followed by the same letter are not significantly different according to the LSD test ($p \le 0.05$)

3.2. Photosynthetic traits

As shown in **Figure 3**, chlorophyll content, Fv/Fm and performance index of faba bean cultivated in saline soil affected significantly (p<0.05) by melatonin levels. In this context, melatonin at a rate of 50 μ M recorded the maximum values of all studied photosynthetic traits achieving increases of 40.6, 6.2 and 74.3% in chlorophyll content, Fv/Fm and performance index, respectively, compared to the control. Also, melatonin at a rate of 100 μ M increased chlorophyll content by 43.8% and Fv/Fm by 5.0%, higher than the control. There were no noticeable variations between 50 and 100 μ M in

3.3. Osmolytes and antioxidants

Application of melatonin caused significant (p<0.05) changes in osmolytes (**Figure 4**) and antioxidants of faba bean plants under salt-affected soil (**Figure 5**). Herein, as melatonin rate increases osmolytes and antioxidants increased. Melatonin at a rate of 100 μ M was the effective treatment for increasing total soluble sugars by 59.9%, proline content by 15.6%, total antioxidant activity (DPPH) by 55.1%, ascorbate (AsA) by 19.7%, glutathione (GSH) by 19.6% and catalase (CAT) by 9.0%, relative to the control treatment. The rate of 50 μ M was as similar as the rate 100 μ M in AsA and GSH.

3.4. Stomatal performance

To have a deep knowledge about the role of foliar application of melatonin in improving faba bean growth, physio-biochemical, and yield-related traits, the stomatal traits in leaf of melatonin and non-melatonin treated plants, were further analyzed. The anatomical measurements were performed in the leaf of control and melatonin-treated plants. Data in (Table 2) showed that stomatal aperture area and stomatal length were increased significantly (p<0.05). The highest increase was observed with melatonin at a rate of 100 μ M treatment (31.1 and 10.7%) followed by the treatment of melatonin at a rate of 50 µM (14.2 and 6.1%). However, stomatal density and stomatal width were not significantly (p>0.05) changed by application of melatonin. Furthermore, it has been found that melatonin application has a high impact on the stomatal aperture as shown in Figure 6.

3.5. Agronomic traits

Generally, all faba bean agronomic traits significantly (p<0.05) improved with melatonin treatment compared to non-treatment (Table 3). The progressive increase in melatonin rate occurred increases in all agronomic parameters. Accordingly, melatonin at a rate of 100 μ M was the remarkable treatment significantly equalling (p>0.05) melatonin at a rate of 50 μ M in plant height, branches number plant-1, pods number plant-1 and seed index. Melatonin at a rate of 100 μM achieved increases of 1.24, 1.38, 1.71, 1.70, 1.63, 1.04, 1.75 and 1.33 folds in plant height, branches number plant-1, leaf area plant-1, plant dry matter, pods number plant-1, seed index green pod yield and dry seed yield, respectively, greater than the control treatment. As well, melatonin at a rate of 50 μ M increased plant height by 22.0%, branches number plant-1 by 47.7%, pods number plant-1 by 57.5%, seed index by 2.7%, green pod yield 30.5% and dry seed yield by 20.3%, compared to no melatonin supply.

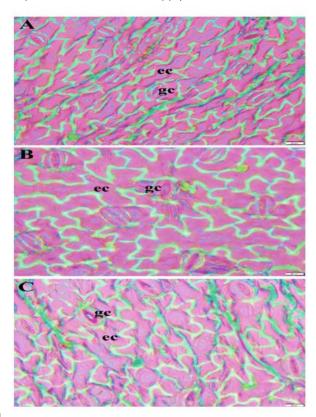


Figure 6. Photographs of leaf abaxial surface of faba bean plant foliar sprayed with melatonin (A) control; (B) melatonin 50 μ M; (C) melatonin 100 μ M. gc, guard cells; ec; Epidermal cells. bars = 20 μ m

4. Discussion

Salinization is a severe global issue, shrinking the crop productivity and causing substantial economic losses in agricultural production (Su *et al.*, 2021; Shaaban *et al.*, 2023; Hadid *et al.*, 2024). Salt stress has adverse impacts on plant growth since physio-biochemical processes are disturbed (Lasheen *et al.*, 2024; Ramadan *et al.*, 2024). However, melatonin as promising molecule could, at least partially, regulate the metabolism and mitigate the saltassociated injuries on faba bean crop cultivated in saline soils. It is possible to highlight this topic via the following explanation and exegeses.

The current study was performed in saline soil with electric conductivity of 7.83 dS m⁻¹ (**Table 1**) and showed negative effects on cell membrane stability and leaf water content of faba bean. Various stresses mainly target the corruption of cell membrane (Saha *et al.*, 2015). Because of salt stress, cellular cytoplasmic constituents and viscidity are altered while lipid peroxidation enhanced (Ali *et al.*, 2020). Measuring cell membrane stability expresses substantially in the behaviour of diverse plant cultivars toward the salt stress (Mahlooji *et al.*, 2017). It has been reported that cell membrane stability significantly associated with relative water content, potassium (K⁺) ions and osmotic adjustment (Shekari *et al.*, 2017). Further, the level of membrane fatty acids saturation and membrane fluidity were changed under salt stress (Farooq and Azam, 2006). On the other

hand, water is the main component related to physiobiochemical reactions for growing plants. Reduction in water absorption is realized under salts stress while hindering relative water content of plant cells (Saha *et al.,* 2015; Meng *et al.,* 2018).

Melatonin level (μM)	Plant height (cm)	Branches number plant ⁻¹	Leaf area plant ⁻¹ (dm ²)	Plant dry matter (g)
0	81.00±4.88b	3.67±0.17b	92.80±1.37b	140.40±2.07b
50	98.83±5.77a	5.42±0.33a	118.90±3.16b	179.80±4.78b
100	100.50±2.65a	5.08±0.47a	158.20±11.94a	239.30±18.05a
	Pod number plant ⁻¹	Seed index (g)	Green pod yield (t ha-1)	Dry seed yield (t ha ⁻¹)
0	13.33±0.63b	94.80±0.22b	12.61±0.31c	2.61±0.01c
50	21.00±0.81a	97.36±1.08a	16.46±0.10b	3.14±0.00b
100	21.83±0.81a	98.63±0.71a	22.09±0.30a	3.49±0.02a

Table 3. Agronomic traits of salt-suffered faba bean as influenced by melatonin concentrations

Values are means \pm standard error; Values in each column followed by the same letter are not significantly different according to the LSD test (p≤0.05).

There is a strong association between photosynthesis rate and plant pigments content. High salt content can adversely influence photosynthetic apparatus via chlorophyll degradation (Wu et al., 2014). Plant leaves showed remarkable decline in different pigments (chlorophyll a, chlorophyll b and carotenoids) under saline conditions (Wu et al., 2014). Chlorophyll disintegration under salinity stress could be ascribed to the activity of chlorophyllase enzyme (Neelesh and Veena, 2015), in addition to the abundant concentration of sodium (Na⁺) and chloride (Cl⁻¹) in plant leaves (Gul et al., 2013). Also, salinity of soil conversely influences photosynthetic activity and induces ROS production, thus declining plant growth and yield. Increased accumulation of ROS is an indication of plant stress for several biochemical molecules involving pigments, lipids and proteins (Mehmood et al., 2019). Furthermore, plants subjected to salinity showed low quantum efficiency in photosystem II (Acosta-Motos et al., 2017). A remarkable correlation has been reported between the amount of Na⁺ ion and chlorophyll fluorescence. Since the ions of Cl⁻¹ and Na⁺ increased in soil solution, their absorption by plants increased while the ions of K⁺, calcium (Ca⁺²) and magnesium (Mg⁺²) decreased (Hu et al., 2016; Mahmud et al., 2017). Based on the ion balance, Cl⁻¹ and Na⁺ toxicity prompt nutritional tumult while rise physiological drought stress by reducing the osmotic potential of the soil solution. Owing to the fluctuation in water potential under salinity, plant suffered osmotic stress (Khan et al., 2019). It has been documented that the assimilation of carbon dioxide via photosynthesis declined with depressing in water potential (Aldesuquy et al., 2014).

Carbohydrates content was depleted in different plant parts owing to salinity stress. Carbohydrates have to adjust cell osmosis since the accumulation of sugars increases via the stimulation of enzymatic sugar hydrolysis under stress conditions (Wang *et al.*, 2013). There was a significant association between stress tolerance and sugar accumulation in several plants (Ali *et al.*, 2018). On the other hand, proline acts a substantial effect for stimulating plant tolerance against environmental stresses. Salinity stress can elevate proline levels and proline increases the enzymatic antioxidant activities via enhancing superoxide dismutase and peroxidase (El-Beltagi and Mohamed *et al.*, 2010; Hu *et al.*, 2016; Devnarain *et al.*, 2016). In this respect, ROS enzymatically scavenged by peroxidase, ascorbate peroxidase, superoxide dismutase, glutathionesynthesizing, catalase, and glutathione reductase. Also, ascorbic acid restored by ascorbate peroxidase and reduced the oxidation (El-Beltagi *et al.*, 2022b; Khan *et al.*, 2018).

As obtained in the current research findings, melatonin improved the cell membrane, leaf water, and photosynthetic traits and regulated the osmolytes, antioxidants activity and stomatal performance in faba bean plants grown in saline soil. In this context, as an adaptive performance plant accumulate noticeable amounts of various osmo-protectants such as proline, soluble sugars and free amino acids under salty stress (Farag et al., 2022). These molecules harmonically work to readjust the osmotic potential of plant cells under stressed conditions, suppressing tissues dehydration and stimulating water uptake (Ramadan et al., 2022). The osmolytes biosynthesis and metabolism under salinity were substantially stimulated with affording melatonin exogenously. Furthermore, application of melatonin induced the activities of antioxidant enzymes, attenuating the ROS accumulation, as well as increased K⁺ content and K^+/Na^+ ratio and Ca^+ content, hence maintaining membrane stability of the stressed cells (El-Bially et al., 2022; El-Metwally et al., 2022). Melatonin regulated the transcription of genes responsible for leaf pigments, keeping photosynthetic proteins and activating the xanthophyll cycle (Yang et al., 2022). Therefore, application of melatonin under saline conditions achieved remarkable increase in leaf pigments while raising the photosynthetic efficiency (Altaf et al., 2020). Since melatonin had a powerful action to adjust of physiological and biochemical constituents of faba bean plants, growth and yield were boosted under salty soil by melatonin supply.

Stomatal traits are important inductors that associated with stress tolerance ability in plants and have critical role in nutrients and water movement in plants (Aebi, 1984; Mohammed *et al.*, 2009; Agami *et al.*, 2016). Melatonin

foliar application improved performance of stomatal traits of faba bean, since the leaf anatomical traits particularly stomatal aperture and area stomatal length were improved. Melatonin foliar spray has important role in strengthening the cell wall and maintained cell expansion for improving the stomata anatomical traits and protecting the chloroplast structure (Mohamed et al., 2020). This improvement in stomatal traits may be due to the role of melatonin for activation of phytohormone that control maintenance of cell turgor pressure and activity of antioxidant defiance system as well as control pro-cambial of vascular tissues (Mohamed et al., 2020). The current results highlighted the great importance of melatonin in improving nutrients and water translocation into active parts of faba bean through enhancing the stomatal performance. Briefly, findings of the current research present obvious insights into the role of melatonin as an enhancer in supporting yield traits through improving photosynthetic apparatus, osmos-regulators defensive antioxidants and stomatal system for sustaining the productivity of faba bean under salty soil situation. Practically, faba bean growers can safely exploit melatonin (100 μ M) to raise the resilience of salt-suffered plants, thus obtaining better productivity and quality.

5. Conclusions

Briefly, findings of the current research present obvious insights into the role of melatonin as an enhancer in supporting yield traits through improving photosynthetic apparatus, osmos-regulators defensive antioxidants and stomatal system for sustaining the productivity of faba bean under salty soil situation. Practically, faba bean growers can safely exploit melatonin (100 μM) to raise the resilience of salt-suffered plants, thus obtaining better productivity and quality. Herein, application of melatonin at 100 μ M improved the economic outcomes of faba bean, i.e. green pod yield and dry seed yield by 75.2 and 33.7%, respectively. Since the 100 µM, as the highest rate tested, revealed the maximum improvement in faba bean performance, further investigations are neded to explore the efficacy of melatonin at other application rates above the 100 μ M, especially its effect at the molecular level.

Acknowledgement

This work was supported by Deanship of Scientific Research, Vice Presidency for Graduate Studies and Scientific Research, King Faisal University, Saudi Arabia (KFU241477), for support this research work.

Data availability

Data presented in current research work are available on request.

Conflicts of interest

The authors declare no conflict of interest.

References

Abd El-Mageed, T.A., Mekdad, A.A.A., Rady, M.O.A., Abdelbaky, A.S., Saudy, H.S., and Shaaban, A. (2022). Physio-biochemical and agronomic changes of two sugar beet cultivars grown in saline soil as influenced by potassium fertilizer. *Journal of Soil Science and Plant Nutrition*, **22**, 3636.

- Abdo, R.A., Hazem, M.M., El-Assar, A.E., Saudy, H.S., El-Sayed, S.M. (2024). Efficacy of nano-silicon extracted from rice husk to modulate the physio-biochemical constituents of wheat for ameliorating drought tolerance without causing cytotoxicity. *Beni-Suef University Journal of Basic and Applied Sciences*, **13**, 75.
- Abou El-Enin, M.M., Sheha, A.M., El-Serafy, R.S., Ali, O.A.M., Saudy, H.S., and Shaaban, A. (2023). Foliage-sprayed nanochitosan-loaded nitrogen boosts yield potentials, competitive ability, and profitability of intercropped maize-soybean. *International Journal of Plant Production*, **17**, 517.
- Acosta-Motos, J.R., Ortuño, M.F., Bernal-Vicente, A., Diaz-Vivancos, P., Sanchez-Blanco, M.J., and Hernandez, J.A. (2017). Plant responses to salt stress: Adaptive mechanisms. *Agronomy* 7, 18. https://doi.org/10.3390/agronomy7010018
- Aebi, H. (1984). Catalase in vitro. Methods Enzymology, 105, 121.
- Agami, R., Medani, R.A., Abd El-Mola, I.A., and Taha, R.S. (2016). Exogenous application with plant growth promoting rhizobacteria (PGPR) or proline induces stress tolerance in basil plants (*Ocimum basilicum* L.) exposed to water stress. *nternational Journal of Environmental and Agriculture Research*, **2**, 78–92.
- Aldesuquy, H., Baka, Z., and Mickky, B. (2014). Kinetin and spermine mediated induction of salt tolerance in wheat plants: Leaf area, photosynthesis and chloroplast ultrastructure of flag leaf at ear emergence. *Egyptian Journal* of Basic and Applied Sciences, **1**, 77.
- Ali, M.A.A., Nasser, M.A., Abdelhamid, A.N., Ali, I.A.A., Saudy, H.S., Hassan, K.M. (2024). Melatonin as a key factor for regulating and relieving abiotic stresses in harmony with phytohormones in horticultural plants — a Review. Journal of Soil Science and Plant Nutrition, 24, 54.
- Ali, S., and Xie, L. (2020). Plant Growth Promoting and Stress mitigating abilities of Soil Born Microorganisms. *Recent Patents on Food, Nutrition and Agriculture*, **11**, 96.
- Ali, S., Khan, N., Nouroz, F., Erum, S., Nasim, W., and Shahid, M.A. (2018). In vitro effects of GA 3 on morphogenesis of CIP potato explants and acclimatization of plantlets in field. *In Vitro Cellular and Developmental Biology*, **54**, 104.
- Altaf, M., Shahid, R., Ren, M., Naz, S., Altaf, M., Qadir, A., Anwar, M., Shakoor, A., and Hayat, F. (2020). Exogenous melatonin enhances salt stress tolerance in tomato seedlings. *Biologia Plantarum*, 64, 604.
- Altaf, M.A., Shahid, R., Ren, M.X., Altaf, M.M., Khan, L.U., Shahid, S., and Jahan, M.S. (2021). Melatonin alleviates salt damage in tomato seedling: A root architecture system, photosynthetic capacity, ion homeostasis, and antioxidant enzymes analysis. *Scientia Horticulturae*, **285**, 110145.
- Ansabayeva, A., Makhambetov, M., Rebouh, N.Y., Abdelkader, M., Saudy, H.S., Hassan, K.M., Nasser, M.A., Ali, M.A.A., Ebrahim, M. (2025). Plant growth-promoting microbes for resilient farming systems: Mitigating environmental stressors and boosting crops productivity — A Review. Horticulturae, 11, 260.
- Arnon, D.I. (1949). Copper enzymes in isolated chloroplasts. polyphenol-oxidase in *Beta vulgaris* L. *Plant Physiology*, 24, 1.
- Bradford, M.M. A (1976). rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the

- Brand-Williams, W., Cuvelier, M.E., and Berset, C. (1995). Use of a free radical method to evaluate antioxidant activity. LWT -Food Science and Technology, 28, 25.
- Clark, A.J., Landolt, W., Bucher, J.B., and Strasser, R.J. (2000). Beech (*Fagus sylvatica*) response to ozone exposure assessed with a chlorophyll a fuorescence performance index. *Environmental Pollution*, **109**, 501.
- Devnarain, N., Crampton, B.G., Chikwamba, R.K., Becker, J.V.W., and O'Kennedy, M.M. (2016). Physiological responses of selected African sorghum landraces to progressive water stress and re-watering. *South African Journal of Botany*, **103**, 61.
- El-Beltagi, H.S., Ahmad, I., Basit, A., Shehata, W.F., Hassan, U., Shah, S.T., Haleema, B. Jalal, A., Amin, R., Khalid, M.A., Noor F., and Mohamed, H.I. (2022a). Ascorbic acid enhances growth and yield of sweet peppers (*Capsicum annum*) by mitigating salinity stress, *Gesunde Pflanzen*, 74, 42.
- El-Beltagi, H.S., El-Yazied, A.A., El-Gawad, H.G.A., Kandeel, M., Shalaby, T.A., Mansour, A.T., Al-Harbi, N.A., Al-Qahtani, S.M., Alkhateeb, A.A., and Ibrahim, M.F.M. (2023). Synergistic impact of melatonin and putrescine interaction in mitigating salinity stress in snap bean seedlings: reduction of oxidative damage and inhibition of polyamine catabolism. *Horticulturae*, 9, 285.
- El-Beltagi, H.S., Mohamed, A.A. (2010). Changes in non protein thiols, some antioxidant enzymes activity and ultrastructural alteration in radish plant (*Raphanus sativus* L.) Grown under lead toxicity. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, **38**(3), 76–85.
- El-Beltagi, H.S., Shah, S., Ullah, S., Sulaiman, Mansour, A.T., and Shalaby, T.A. (2022b). Impacts of ascorbic acid and alphatocopherol on Chickpea (*Cicer arietinum* L.) grown in water deficit regimes for sustainable production. *Sustainability*, **14**, 8861.
- El-Bially, M.A., El-Metwally, I.M., Saudy, H.S., Aisa, K.H., Abd El-Samad, G.A. (2023). Mycorrhiza-inoculated biochar as an ecofriendly tool improves the broomrape control efficacy in two faba bean cultivars. *Rhizosphere*, **26**, 100706.
- El-Bially, M.A., Saudy, H.S., Hashem, F.A., El–Gabry, Y.A., and Shahin, M.G. (2022). Salicylic acid as a tolerance inducer of drought stress on sunflower grown in sandy soil. *Gesunde Pflanzen*, **74**, 603.
- El-Metwally IM, Saudy HS, and Elewa T.A. (2022). Natural plant by-products and mulching materials to suppress weeds and improve sugar beet (*Beta vulgaris* L.) yield and quality. *Journal* of Soil Science and Plant Nutrition, **22**, 5217.
- Emam, T.M., Hosni, A.M., Ismail, A., El-Kinany, R.G., Hewidy, M., Saudy, H.S., Omar, M.M.A., Ibrahim, M.T.S., Sui Shunzhao, Elsayed, S.M. (2025). Physiological and molecular responses of red amaranth (Amaranthus cruentus L.) and green amaranth (Amaranthus hypochondriacus L.) to salt stress. *Journal of Soil Science and Plant Nutrition*, **25**, 171.
- Farag, H.A., Ibrahim, M.F., El-Yazied, A., El-Beltagi, H.S., El-Gawad, H.G.A., Alqurashi, M., Shalaby, T.A., Mansour, A.T., Alkhateeb, A.A., and Farag, R. (2022). Applied selenium as a powerful antioxidant to mitigate the harmful effects of salinity stress in snap bean seedlings. *Agronomy*, **12**, 3215.
- Farooq, S., and Azam, F. (2006). The use of cell membrane stability (CMS) technique to screen for salt tolerant wheat varieties. *Journal of Plant Physiology*, **163**, 629.

- Gomez, K.A., and Gomez, A.A. (1984). Statistical Procedures for Agricultural Research. *John Wiley Sons Inc* 20–212.
- Gul, B., Ansari, R., Flowers, T.J., and Khan, M.A. (2013). Germination strategies of halophyte seeds under salinity. *Environmental and Experimental Botany*, 1, 4.
- Hadid, M.L., Abd El-Mageed, T.A., Ramadan, K.M.A., El-Beltagi H.S., Alwutayd, K.M., Hemida, K.A., Shalaby, T.A., Al-daej, M.I., Saudy, H.S., Al-Elway, O.A.A.I. (2024). Pyridoxine-HCl plus gypsum and humic acid reinforce salinity tolerance of coriander plants with boosting yield and modifying oil fractionations. *Russian Journal of Plant Physiology*, **71**, 64.
- Hadid, M.L., Ramadan, K.M.A., El-Beltagi, H.S., Ramadan, A.A., El-Metwally, I.M., Shalaby, T.A., Bendary, E.S.A., and Saudy, H.S. (2023). Modulating the antioxidant defense systems and nutrients content by proline for higher yielding of wheat under water deficit. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, **51**, 13291.
- Hayat, S., Hayat, Q., Alyemeni, M.N., Wani, A.S., Pichtel, J., and Ahmad A. (2007). Role of proline under changing environments: A review. *Plant Signaling and Behavior*, 7, 1456.
- Helal, N.M., Saudy, H.S., Hamada, M.M.A., El-Yazied, A.A., Abd El-Gawad, H.G., Mukherjee, S., Al-Qahtani, S.M., Awad A.N., El-Sayed, S.M., Ibrahim, M.F.M. (2024). Potentiality of melatonin for reinforcing salinity tolerance in sorghum seedlings via boosting photosynthetic pigments, ionic and osmotic homeostasis and reducing the carbonyl/oxidative stress markers. Journal of Soil Science and Plant Nutrition, 24, 4243.
- Hu, Y., Xia, S., Su, Y., Wang, H., Luo, W., Su, S., and Xiao, L. (2016).
 Brassinolide increases potato root growth in vitro in a dosedependent way and alleviates salinity stress. *BioMed Research International*, **2016**, 8231873.
- Irigoyen, J.J., Emerich, D.W., and Sanchez-Diaz, M. (1992). Water stress induced changes in the concentrations of proline and total soluble sugars in nodulated alfalfa (*Medicago sativa*) plants. *Plant Physiology*, 84, 55.
- Jensen, N.B., Ottosen, C.O., and Zhou, R. (2023). Exogenous melatonin alters stomatal regulation in Tomato seedlings subjected to combined heat and drought stress through mechanisms distinct from ABA signaling. *Plants*, **12**, 1156.
- Khan, N., and Bano, A. (2018). Effects of exogenously applied salicylic acid and putrescine alone and in combination with rhizobacteria on the phytoremediation of heavy metals and chickpea growth in sandy soil. *International Journal of Phytoremediation*, **16**, 405.
- Khan, N., Bano, A., and Babar, M.A. (2019). The stimulatory effects of plant growth promoting rhizobacteria and plant growth regulators on wheat physiology grown in sandy soil. *Archives* of Microbiology, 201, 769.
- Klute, A., and Dirksen, C. (1986). Hydraulic conductivity and diffusivity: laboratory methods, in Methods of Soil Analysis: Part 1-Physical and Mineralogical Methods, (Madison: Soil Science Society of America, American Society of Agronomy). 28, 687.
- Lasheen, F.F., Hewidy, M., Abdelhamid, A.N., Thabet, R.S., Abass, M.M.M., Fahmy, A.A., Saudy, H.S., Hassan, K.M. (2024). Exogenous application of humic acid mitigates salinity stress on pittosporum (Pittosporum tobira) plant by adjusting the osmolytes and nutrient homeostasis. *Gesunde Pflanzen*, **76**, 317.
- Mahlooji, M., Seyed Sharifi, R., Razmjoo, J., Sabzalian, M.R., and Sedghi, M. (2017). Effect of salt stress on photosynthesis and

physiological parameters of three contrasting barley genotypes. *Photosynthetica*, **56**, 549.

- Mahmud, S., Sharmin, S., Chowdhury, B.L., and Hossain, M.A. (2017). Effect of salinity and alleviating role of methyl jasmonate in some Rice varieties. *Asian Journal of Plant Science*, **16**, 87.
- Maxwell K, and Johnson GN. (2000). Chlorophyll fuorescence a practical guide. *Journal of Experimental Botany*, **51**, 659–668.
- Mehmood, A., Hussain, A., Irshad, M., Hamayun, M., Iqbal, A., and Khan, N. (2019). In vitro production of IAA by endophytic fungus Aspergillus awamori and its growth promoting activities in *Zea mays. Symbiosis*, **77**, 225.
- Meng, X., Zhou, J., and Sui, N. (2018). Mechanisms of salt tolerance in halophytes: Current understanding and recent advances. Open Life Sciences, 13, 149.
- Mohamed, A.A, El-Beltagi, H.S, and Rashed, M.M. (2009). Cadmium stress induced change in some hydrolytic enzymes, free radical formation and ultrastructural disorders in radish plant, *Electronic Journal of Environmental, Agricultural and Food Chemistry*, 8, 969.
- Mohamed, I.A.A., Shalby, N., El-Badri, A.M.A., Saleem, M.H., Khan, M.N., Nawaz, M.A., Qin, M., Agami, R.A., Kuai, J., and Wang, B. (2020). Stomata and xylem vessels traits improved by melatonin application contribute to enhancing salt tolerance and fatty acid composition of Brassica napus L. plants. Agronom, y 10, 1186.
- Mukherjee, S.P., and Choudhuri, M.A. (1983). Implications of water stress induced changes in the levels of endogenous ascorbic acid and hydrogen peroxide in Vigna seedlings. *Physiologia Plantarum*, 58, 166.
- Neelesh, K., and Veena, P. (2015). Effect of salt stress on growth parameters, moisture content, relative water content and photosynthetic pigments of Fenugreek variety RMt-1. *Journal of Plant Science*, **10**, 210.
- Page, A.L., Miller, R.H., and Keeny, D.R. (1982). Methods of soil analysis, in Part II. Chemical and Microbiological Methods.
 2nd Edn, eds A. L. Page, R. H. Miller, D. R. Keeney, D. E. Baker, R. H. Miller, R. Ellis Jr., *et al.* (Madison, WI: American Society of Agronomy). **1159**, 225.
- Pan, Y., Xu, X., Li, L., Sun, Q., Wang, Q., Huang, H., Tong, Z., and Zhang, J. (2023). Melatonin-mediated development and abiotic stress tolerance in plants. *Frontiers in Plant Science*, 14, 1100827.
- Premachandra, G.S., Saneoka, H., and Ogata, S. (1990). Cell membrane stability, an indicator of drought tolerance, as affected by applied nitrogen in soybean. *Journal of Agricultural Science*, **115**, 63.
- Ramadan, K.M.A., Alharbi, M.M., Alenzi, A.M., El-Beltagi, H.S., Darwish, D.B., Aldaej, M.I., Shalaby, T.A., Mansour, A.T., El-Gabry, Y.A., and Ibrahim, M.F.M. (2022). Alpha lipoic acid as a protective mediator for regulating the defensive responses of wheat plants against sodic alkaline stress: Physiological, biochemical and molecular aspects. *Plants*, **11**, 787.
- Ramadan, K.M.A., El-Beltagi, H.S., Abd El-Mageed, T.A.A, Saudy, H.S., Al-Otaibi, H.H., Mahmoud, M.A.A. (2023a). The changes in various physio-biochemical parameters and yield traits of faba bean due to humic acid plus 6-benzylaminopurine application under deficit irrigation. Agronomy, 13, 1227.
- Ramadan, K.M.A., El-Beltagi, H.S., Al Saikhan, M.S., Almutairi, H.H., Al-Hashedi, S.A., Saudy, H.S., Al-Elwany, O.A.A.I., Hemida, K.A., Abd El-Mageed, T.A., Youssef, S.M. (2024). β-carotene supply to

dill plants grown in sulphur and humic acid-amended soil improves salinity tolerance via quenching the hazard molecules. *Russian Journal of Plant Physiology*, **71**, 45.

- Ramadan, K.M.A., El-Beltagi, H.S., El-Mageed, T.A.A., Saudy, H.S., Al-Otaibi, H.H., and Mahmoud, M.A.A. (2023b). The changes in various physio-biochemical parameters and yield traits of Faba bean due to humic acid plus 6-benzylaminopurine application under deficit irrigation. Agronomy, 13, 1227.
- Ramadan, K.M.A., El-Beltagi, H.S., Makhlouf, B.S.I., Khalil, S.R.A., Al-Daej, M.I., Shalaby, T., Bendary, E.S.A. and Saudy, H.S. (2025). Carboxymethyl chitosan improves sugar beet tolerance to drought by controlling enzyme activity and stomatal conductance. *Polish Journal of Environmental Studies*, **34**, 791.
- Selvanarayanan, R., Rajendran, S., Algburi, S., Khalaf, O.I., Hamam,
 H. (2024). Empowering coffee farming using counterfactual recommendation based RNN driven IoT integrated soil quality command system. *Scientific Reports* 14, 6269
- Rizk, T.Y., Kholousy, A.S.O., Saudy, H.S., Sultan, S.H.S., and Abd Alwahed, S.H.A. (2023). Breaking dormancy and enhancing germination of *Avena sterilis* L. and Amaranthus retroflexus L. weeds by gibberellic acid and potassium nitrate to keep soil and crops healthy. *Gesunde Pflanzen*, **75**, 757.
- Saha, J., Brauer, E.K., Sengupta, A., Popescu, S.C., Gupta, K., and Gupta, B. (2015). Polyamines as redox homeostasis regulators during salt stress in plants. *Frontiers in Environmental Science*, 3, 21.
- Saudy, H.S., El-Metwally, I.M., Sobieh, S.T., Abd-Alwahed, S.H.A. (2022). Mycorrhiza, charcoal, and rocket salad powder as ecofriendly methods for controlling broomrape weed in interplanted faba bean with flax. Journal of Soil Science and Plant Nutrition, 22, 5195.
- Saudy, H.S., Hamed, M.F., El–Metwally, I.M., Ramadan, K.M.A., Aisa, K.H0 (2021). Assessing the effect of biochar or compost application as a spot placement on broomrape control in two cultivars of faba bean. *Journal of Soil Science and Plant Nutrition*, 21, 1856.
- Saudy, H.S., Noureldin, N.A., Mubarak, M., Fares, W., Elsayed, M. (2020). Cultivar selection as a tool for managing soil phosphorus and faba bean yield sustainability. Archives of Agronomy and Soil Science, 66, 414.
- Shaaban, A., Abd El-Mageed, T.A., Abd El-Momen, W.R., Saudy, H.S., Al-Elwany, O.A.A.I. (2023). The integrated application of phosphorous and zinc affects the physiological status, yield and quality of canola grown in phosphorus-suffered deficiency saline soil. *Gesunde Pflanzen*, **75**, 1813.
- Shabbir, R., Singhal, R.K., Mishra, U.N., Chauhan, J., Javed, T., Hussain, S., Kumar, S., Anuragi, H., Lal, D., and Chen, P. (2022). Combined abiotic stresses: Challenges and potential for crop improvement. *Agronomy*, **12**, 2795.
- Sharma, A., Shahzad, B., Kumar, V., and Kohli, S.K. (2019). Phytohormones regulate accumulation of osmolytes under abiotic stress. *Biomolecule*, 9, 284.
- Sharma, S. S., and Dietz, K. J. (2009). The relationship between metal toxicity and cellular redox imbalance. *Trends in Plant Science*, **14**, 43.
- Shekari, F., Abbasi, A., and Mustafavi, S.H. (2017). Effect of silicon and selenium on enzymatic changes and productivity of dill in saline condition. *Journal of the Saudi Society of Agricultural Sciences*, 1, 367.

- Su, J., Yang, X., Shao, Y., Chen, Z., and Shen, W. (2021). Molecular hydrogen–induced salinity tolerance requires melatonin signalling in Arabidopsis thaliana. *Plant Cell Environment*, 44, 476.
- Van Zelm, E., Zhang, Y., and Testerink, C. (2020). Salt tolerance mechanisms of plants. *Annual Review of Plant Biology*, **71**, 403.
- Wang, M., Zheng, Q., Shen, Q., and Guo, S. (2013). The critical role of potassium in plant stress response. *International Journal of Molecular Sciences*, 14, 7370.
- Wang, Y., Zhao, H., Hu, X., Zhang, Y., Zhang, Z., Zhang, L., Li, L., Hou, L., and Li, M. (2022). Transcriptome and hormone analyses reveal that melatonin promotes adventitious rooting in shaded cucumber hypocotyls. *Frontiers in Plant Science*, **13**, 1059482.

Wu, X., He, J., Chen, J., Yang, S., and Zha, D. (2014). Alleviation of

exogenous 6-benzyladenine on two genotypes of eggplant (*Solanum melongena* Mill.) growth under salt stress. *Protoplasma*, **251**, 169.

- Yashodha, G., Rajakumar, B., Krishnamoorthy, M., Surendran, R. (2025). Efficient Plant Disease Detection using K-Means clustering and DenseNet-based Classification, International Conference on Electronics and Renewable Systems (ICEARS), Tuticorin, India, 1197–1204.
- Yang, L., You, J., Li, J., Wang, Y., and Chan, Z. (2021). Melatonin promotes Arabidopsis primary root growth in an IAAdependent manner. *Journal of Experimental Botany*, **72**, 5599.
- Yang, S., Zhao, Y., Qin, X., Ding, C., Chen, Y., Tang, Z., Huang, Y., Reiter, R.J., Yuan, S., and Yuan, M. (2022). New insights into the role of melatonin in photosynthesis. *Journal of Experimental Botany*, **73**, 5918.