

Mitigating the oxidative stress caused by UV-B in date palm seedlings: efficacy of salicylic acid and ascorbic acid application

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Abstract

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The date palm is one of the plants whose growth is being affected by global warming through harmful wavelengths of UV radiation. The protective role of salicylic acid (SA) and ascorbic acid (AsA) at physiological (100 and 200 mg l⁻¹) levels was assessed under UV-B (8 hrs day⁻¹) stress in the development and physiological adaptation of date palm seedlings. Three months after treatment with different concentrations of SA and AsA, their effects on growth criteria, pigment content, oxidation stress markers, and enzyme antioxidant activities were studied. Results revealed that both SA and AsA increased the seedling height, leaf width, and dry weight, decreased the level of malondialdehyde and hydrogen peroxide, and increased membrane stability, thereby alleviating oxidant injury. Furthermore, activities of antioxidant enzymes such as peroxidase and ascorbate peroxidase have been upregulated, thereby enhancing the seedlings' tolerance against stress. The results suggest that foliar SA and AsA application could be an efficient way to alleviate the UV-B radiation stress damage in young date palm plants, therefore providing a possible approach to improving crop resilience in increasingly harsh environmental conditions.

Keywords

antioxidant enzymes, ascorbic acid, oxidative stress, *Phoenix dactylifera* L., salicylic acid, UV-B

Introduction

Date palm (*Phoenix dactylifera* L.) is among the prominent plants cultivated in the Middle East and North Africa region part of the globe and provides feeding for people from arid and semi-arid regions (BENACEUR et al., 2024). The date palm is well-known for its precious nutritional importance and resistance to environmental stressors such as high temperature and drought (AL-KARMADI and OKOH, 2024). Even though this plant is hardy, the date palm is not sheltered from abiotic stress, especially the increment of ultraviolet (UV) radiation due to ozone layer depletion (SWAID and ALI, 2024).

Among the different wavelengths of UV radiation, UV-B (280–315 nm) is particularly harmful to plant health. UV-B exposure damages cellular structures and

triggers the accumulation of highly reactive and unstable reactive oxygen species (ROS), including superoxide radicals, hydroxyl radicals, and hydrogen peroxide (BARNES et al., 2023). Such ROS can cause oxidative stress, which can harm vital cellular components such as lipids, proteins, and nucleic acid and negatively affect the physiological functions and growth of plants (KESAWAT et al., 2023). All this oxidative stress is affecting the physiological functions of plants instead of growing them.

Plants evolved elaborate defence mechanisms against oxidative stress. Antioxidants, such as salicylic acid (SA) and ascorbic acid (AsA), are therefore at the centre of these mechanisms, being involved in the detoxification of ROS and limitation of oxidative damage (RAHMAN et al., 2024). SA is a natural phenol compound that is involved in plant defence, growth regulation, and responses to stress.

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It is involved in the activation of key ROS-scavenging antioxidant enzymes, including peroxidase (POD) and ascorbate peroxidase (APX) (SANGWAN et al., 2022). Similar to tocopherol, ascorbic acid, also known as vitamin C, is another vital antioxidant in plants since it can scavenge ROS directly and regenerate other antioxidants such as tocopherol and glutathione (ABDULLAH et al., 2023a). It has been reported that foliar sprays of AsA improve plant tolerance to multiple abiotic stresses (KHAZAEI et al., 2020), including UV radiation, through the elevation of antioxidant enzyme activity and the increase in photoprotection efficiency.

Studies have shown that exogenous treatments with SA and AsA can alleviate damage from environmental stress and preserve chlorophyll from photooxidation. SA reduces salt stress in cowpea seedlings (SOUSA et al., 2024) and salinity, as well as drought stress in *Triticum aestivum* (TAJDARI et al., 2024). The references of AsA and SA on frost stress in *Vitis vinifera* (JALILI et al., 2023), AsA on Indian almond under heat stress (ABDULLAH et al., 2023b), AsA and SA on *Glycine max* L. under UV-B stress. Finally, SWAID et al. (2020b) found that the morphological defense system characteristics of palm species, including *Phoenix dactylifera* L. and *Washingtonia filifera*, were affected by UVB doses. The results showed that 2 h of UV-B exposure had a positive effect on morphological traits and biomass. Conversely, 4–10 h of UV exposure had detrimental effects on these traits. However, these low levels of UV did not affect morphology or mass.

Although extensive information is available regarding the individual mechanism of action of salicylic acid (SA) and ascorbic acid (AsA), there is a warrant to explore the interplay of these compounds in response to UV-B stress in date palm seedlings. As UV radiation increases and poses a threat to date palm cultivation, looking for alternatives to enhance its tolerance is becoming necessary. Hence, this study developed date palm seedlings under UV stress and aimed to evaluate the effects of various concentrations of salicylic (SA) and ascorbic acid (AsA) on growth, physiological, and biochemical responses.

Materials and methods

In 2023, a laboratory experiment was performed at the photo-stress and ultraviolet radiation laboratory, College of Sciences, University of Basrah, to investigate the effects of salicylic acid (SA) and ascorbic acid (AsA) on the growth characteristics and physiological responses of *Phoenix dactylifera* L. (cv. Hellawi) seedlings under UV-B stress. The seeds of the Hellawi cultivar were planted in the wooden shade using plastic pots containing a mixture of clay, peat moss, and vermiculite (1:1:1) individually for each plant pot. The pots were watered as needed manually. The hogland nutrient solution was used every ten days.

After the seedlings reached one year of age, they were transferred to the laboratory for experiment. In the laboratory, an incubator was used with its inner walls covered with light-reflecting paper to ensure light distribution in all directions. The incubator consisted of small rooms.

Each chamber was equipped with a lamp as a source of ultraviolet radiation type B with a power of 30 watts and a wavelength of (280–320 nm). This source of ultraviolet radiation was fixed between 4 fluorescent lamps as a source of standard white light suitable for plant growth and within the effective light spectrum for the radiation active photosynthesis (PAR) process in the upper part of the incubator and 80 cm away from the plant. All plants used in this study were incubated at a temperature of 30 °C, relative humidity of 50–60%, and a light intensity of 500 $\mu\text{mol/s/12}$ hours per day. The seedlings were exposed to the treatments using electronic timers under 12 hrs of dark and 12 hrs of light day, including ultraviolet radiation (UV-B) (8 hours a day). All seedlings were shortened to 20 cm before the start of the spraying operation. The seedlings were sprayed (50 ml) with salicylic acid at 100 and 200 mg l^{-1} and ascorbic acid at 100 and 200 mg l^{-1} to each plant twice weekly in March. Treatments included Co.1; Control with white light only, Co.2; Control with white light and UV-B light, SA100; Salicylic acid 100 mg l^{-1} under UV-B and white light, SA 200; Salicylic acid 200 mg l^{-1} under UV-B and white light, AsA 100; Ascorbic acid 100 mg l^{-1} under UV-B and white light, AsA 200; Ascorbic acid 200 mg l^{-1} under UV-B and white light. The seedlings were harvested three months after the antioxidant application. Five seedlings were used per treatment to analyze.

Growth parameters

The seedlings' height was measured by determining the distance from the soil level to the tip of the plant, using centimetres as the unit of measurement. The width of each leaf was measured, and the length was recorded in centimeters. Afterward, the plants were rinsed thoroughly and then oven-dried at 75 °C for 48 hours to determine their dry mass. Once dried, the samples were weighed, and the results were expressed in grams.

Estimation of photosynthetic pigments

Fresh date palm leaves were ground and harvested for the determination of pigment content, following HORWITZ and LATIMER (2005) method. Two hundred milligrams of leaf tissues of each sample were homogenized with 8 mL of 80% acetone and centrifuged at $3,000 \times g$ for 3 minutes. Total chlorophyll, anthocyanins, and carotenoids were measured at wavelengths of 645 and 663 nm, 553 nm, and 470 nm, respectively, from the supernatant, according to ZAEHRINGER et al. (1974).

Malondialdehyde content (MDA)

Malondialdehyde (MDA) reflects the level of lipid peroxidation and was measured by grinding fresh leaf tissue (0.5–1.0 g) in 5 ml of 5% trichloroacetic acid. For only 15 minutes at room temperature, the mixture was centrifuged at $6,000 \times g$. The extract obtained was further mixed with thiobarbituric acid and then centrifuged for another 5 min. Absorbance was read at 532 nm, with adjustments made

for any background interference. MDA content was calculated using an extinction coefficient of $155 \text{ mM}^{-1} \text{ cm}^{-1}$, as described by HEATH and PACKER (1968).

Hydrogen peroxide content (H_2O_2)

For hydrogen peroxide measurement, 50 mg of leaf tissue was homogenized in 3 ml of phosphate buffer solution (50 mM, pH 6.5) and centrifuged at $8,000 \times g$ for 20 minutes. A 3 ml aliquot of the resulting extract was then mixed with 1 ml of 0.1% titanium sulfate in 20% sulfuric acid. The yellow colour was quantified at 410 nm after centrifugation again ($7,000 \times g$ for 10 min). H_2O_2 concentration was determined according to KANWAL et al. (2014) based on an extinction coefficient of $0.28 \mu\text{mol}^{-1} \text{ cm}^{-1}$.

Membrane stability index (MSI)

Membrane stability fresh leaves (1 g) of each treatment were diced and immersed in 10 ml deionized water on a vibrating plate at room temperature (25°C) for 24 h after incubation. The first electrical conductivity (C1) was recorded. Subsequently, they were kept for a total of 2 h in an autoclave at a temperature of 90°C to free the entire mixture and, after that, cooled back to the temperature of 25°C , recording a second reading (C2) on electrical conductivity. According to LUTTS et al. (1995), the membrane stabilization index was calculated using the following calculation: $\text{MSI}\% = [1 - C1 / C2] \times 10$.

Soluble protein content

Homogenates were prepared from fresh leaf tissue (200 mg) by grinding in 5 ml potassium phosphate buffer (pH 7), and the homogenate was centrifuged ($17,000 \times g$, 20 min.) and transferred supernatant into test tubes. The content of soluble protein was determined according to the method proposed by Bradford (BRADFORD et al., 1976), using bovine serum albumin as standard. It provides a simple and rapid way of estimating the concentration of proteins from plant materials.

Analyzing the quantity of antioxidant enzymes

For the determination of antioxidant enzyme activity, leaf samples were ground in liquid nitrogen, keeping the same conditions to prevent wilting and maintaining enzyme activity. Isolation of enzymes: 0.5 g leaf tissue was ground in cold acetone ($0-4^\circ\text{C}$) to keep the enzyme activity intact and incubated in a buffer solution before analysis. The activity of POD was evaluated based on NAKANO and ASADA (1980). In this test, 3 ml of the reaction mixture containing 2.85 ml of 3% guaiacol (dissolved in water), 0.1 ml of 2% hydrogen peroxide (H_2O_2), and the enzyme extract (50 μl) was used. The absorbance changes were measured at 470 nm, and the activity was expressed based on the apparent absorbance coefficient of guaiacol at this wavelength. That gives us the peroxidase activity and, therefore, the performance of the antioxidant system in stressed plants. The

enzyme reaction solution includes 2.85 ml of the guaiacol (3%, aqueous solution), 0.1 ml of H_2O_2 (2%), and 50 μl of extraction enzymes. The activity unit was defined based on the guaiacol absorbance coefficient at 470 nm per ml. The activity unit was established according to the absorbance coefficient of guaiacol at 470 nm. The enzyme activity were subsequently quantified as enzyme units per gram of fresh weight ($\text{U g}^{-1} \text{ FW}$). The APX activity was determined using the NAKANO and ASADA (1981) method, which relies on the decrease of oxidized ascorbate at 290 nm.

Statistical analysis

The data was analyzed using a completely random design. The statistical analysis was conducted using the IBM-SPSS-23 software (Chicago, Illinois, USA) using the ANOVA table, and the average differences were determined using the Duncan test at $P > 0.01$.

Results

Growth parameters

As shown in Table 1, seedlings' growth was significantly influenced by different concentrations of SA and AsA applied. The maximum leaf width (1.5 cm) was recorded for 200 mg l^{-1} SA, while the minimum (0.87 cm) was for control under UV-B light (Co.2), confirming the efficacy of UV-B stress. Seedling height was highest at 100 mg l^{-1} SA (40.67 cm) and slightly lower in height at 200 mg l^{-1} SA (39.12 cm) compared to the control (22 cm) affected by the UV-B treatment. Among these, the biomass was highest at 100 mg l^{-1} SA (12.49 g), which exhibited the ability of SA to enhance biomass under stresses, and lowest for the UV-B control (7.6 g). The effects of AsA improvements in growth parameters were obtained by AsA treatments, with 200 mg l^{-1} AsA being significantly higher in leaf width and leaf dry weight compared to the UV-B control but lower than SA treatments. In summary, SA at 100 mg l^{-1} was the most effective treatment for all parameters measuring the impact of UV-B stress on date palm seedlings and appears to be more effective than AsA and controls in alleviating the effects of UV-B stress on date palm seedlings.

Pigments content

The effect of SA and AsA application on the pigment content of date palm seedlings grown under UV-B stress is shown in Table 2. The maximum content of total chlorophyll (14.26 mg g^{-1}) was observed in control under white light only (Co.1) compared with 100 mg l^{-1} of SA (15.3 mg g^{-1}) and 200 mg l^{-1} (14.21 mg g^{-1}), confirming the protective effect of former two treatments against UV-B stress. The chlorophyll contents of the control (Co.1) and treated (Co.2) (only UV-B exposure) were noted as 21.82 and 10.46 mg g^{-1} , respectively, exhibiting the detrimental effects of UV-B stress. Total carotenoid content was highest in the control under UV-B (0.180 mg g^{-1}) and lower in

Table 1. Effect of salicylic acid (SA) and ascorbic acid (AsA) on the growth parameters of the date palm seedlings growing under the UV-B light stress (8 hrs day⁻¹)

Treatments	Leaf width (cm)	Seedling height (cm)	Dry weight (g)
Co.1	1.29 ± 0.05b	33.00 ± 0.03b	11.19 ± 0.08c
Co.2	0.87 ± 0.02c	22.00 ± 0.02c	7.60 ± 0.06c
SA 100 mg l ⁻¹	1.15 ± 0.02b	40.67 ± 0.13a	12.49 ± 0.13a
SA 200 mg l ⁻¹	1.5 ± 0.04a	39.12 ± 0.03a	11.43 ± 0.09b
AsA 100 mg l ⁻¹	1.17 ± 0.03b	25.00 ± 0.02c	10.36 ± 0.09d
AsA 200 mg l ⁻¹	1.27 ± 0.04b	32.00 ± 0.02b	11.18 ± 0.08c

Co.1: Control with white light only; Co. 2: Control with white light and UV-B light. Indicates the average of 5 repeated experiments with the standard deviation (SD) included. Means with distinct letters are statistically different at a significance level of $p < 0.01$, as determined by the Duncan test.

Table 2. Effect of salicylic acid (SA) and ascorbic acid (AsA) on pigments content in leaves of date palm seedlings exposure to the UV-B light stress (8 hrs day⁻¹)

Treatments	Total chlorophyll content (mg g ⁻¹)	Carotenoids content (mg g ⁻¹)	Anthocyanin content (mg g ⁻¹)
Co.2	10.46 ± 0.02c	0.180 ± 0.02a	2.01 ± 0.01a
SA100 mg l ⁻¹	15.30 ± 0.04a	0.150 ± 0.13bc	1.51 ± 0.2bc
SA200 mg l ⁻¹	12.10 ± 0.02b	0.171 ± 0.03ab	1.62 ± 0.02b
AsA 100 mg l ⁻¹	12.32 ± 0.03b	0.141 ± 0.02c	1.39 ± 0.01c
AsA 200 mg l ⁻¹	14.21 ± 0.04a	0.143 ± 0.02c	1.89 ± 0.02a

Co.1: Control with white light only; Co.2: Control with white light and UV-B light. Indicates the average of 5 repeated experiments with the standard deviation (SD) included. Means with distinct letters are statistically different at a significance level of $p < 0.01$, as determined by the Duncan test.

the other treatments, although the 200 mg l⁻¹ SA treatment remained relatively high at 0.171 mg⁻¹, therefore possibly indicative of an adaptive response. Both the white light control and the UV-B control showed the highest anthocyanin content (1.82 and 2.01 mg g⁻¹, respectively); the result in SA and AsA treatments reduced it, especially in 100 mg l⁻¹ AsA (1.39 mg g⁻¹). In general, SA and AsA application (notably 100 mg l⁻¹ SA) sustained chlorophyll contents under stress, but the responses of carotenoids and anthocyanin were ambiguous due to the possibly distinct mechanisms of adaptation to stress.

Oxidative stress and membrane stability

Applying SA and AsA at different concentrations significantly influenced oxidative stress markers like malondialdehyde (MDA) and hydrogen peroxide (H₂O₂), as well as membrane stability (Fig. 1). MDA content in UV-B exposed in the control (Co.2) increased, as compared to white light control (Co.1). Conversely, significantly lower levels of MDA were observed in 100 mg l⁻¹ and 200 mg l⁻¹ SA treatments compared to the control group, indicating the possible protective role of SA treatments in reducing lipid peroxidation under stress. Likewise, H₂O₂ content was higher in UV-B control, and both SA and AsA treatments, especially at 100 mg l⁻¹, decreased H₂O₂ due to alleviation of oxidative injury. However, under UV-B control, membrane stability was severely damaged, and this damage was significantly restored by SA 100 mg l⁻¹, as well as by SA 200 mg l⁻¹, indicating that SA is an effective protector against damage caused by UV-B stress. SA (100

mg l⁻¹) was more effective in increasing membrane stability and in reducing the oxidative markers, indicating that it may be an effective protectant of date palm seedlings under UV-B stress.

Biochemical markers and antioxidant enzyme activities

Figure 2 shows the effects of salicylic acid (SA) and ascorbic acid (AsA) on soluble protein, peroxidase activity, and ascorbate peroxidase (APX) activity of date palm seedlings under UV-B stress. The soluble protein amount was significantly higher in control under white light than in the UV-B control (Co. 2), indicating that the protein cannot be high under the UV-B condition due to the retraction of protein by exposure to UV-B. Under UV-B, the levels of proteins significantly increased on the treatments of 100 mg l⁻¹ and 200 mg l⁻¹ SA, and 200 mg l⁻¹ AsA, with 100 mg l⁻¹ showing the most profound effect, which indicates its role in protein stabilization under stress. The highest peroxidase activity observed in the UV-B control suggests that this stress enhanced the antioxidant response. Conversely, the peroxidase activity decreased as a result of SA and AsA treatments, with 100 mg l⁻¹ SA showing an intermediate level of balance, possibly suggesting an enhanced antioxidant defence. Among the treatments, SA (particularly 100 mg l⁻¹) resulted in a significant increase in APX, indicating SA can enhance the activity of this enzyme as a part of the plant enzymatic defence. Finally, SA was able to safeguard oxidative stress in date palm seedlings under UV-B by

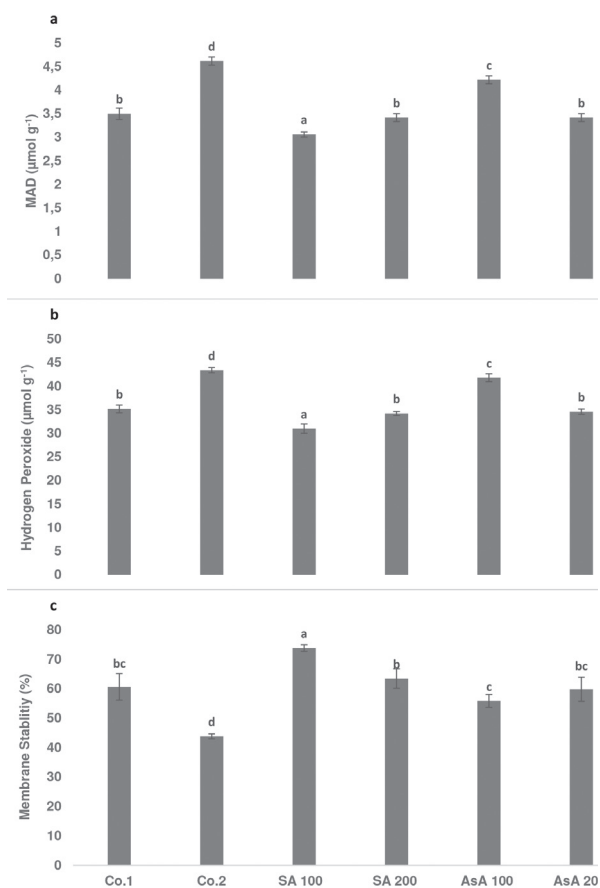


Fig. 1. Effect of salicylic acid (SA) and ascorbic acid (AsA) on MDA (a), hydrogen peroxide (b), and membrane stability (c) of the date palm seedlings growing under the UV-B light stress. Co.1: Control with white light only; Co.2: Control with white light and UV-B light. The averages of 5 samples \pm SD. Columns containing various letters are significantly distinct at $p \leq 0.01$ after the Duncan test.

generally reinforcing protein content and inducing anti-oxidant enzyme activations, especially at 100 mg l⁻¹.

Discussion

The current findings evidently showed that the exogenous salicylic acid (SA) and ascorbic acid (AsA) were effective in reducing the stress effects of UV-B radiation on the growth physiological and biochemical mechanisms of date palm seedlings. These findings align with a recent study that stressed the significance of antioxidant biosynthesis for overcoming oxidative stress and promoting tolerance in plants to adverse conditions (ARSULE et al., 2024).

The significant enhancement in leaf width, seedling height, and dry weight with SA and AsA treatment (Table 1) illustrates the characteristic growth-promoting effect of the RA-possessing plant hormone SA under stressed conditions. These findings show that the effect of SA and AsA also participates in both the allelopathic damage reduction to protect plants from oxidative injury and the essential development of plants at sub-optimal environmental conditions. SA has been shown to regulate several physiological

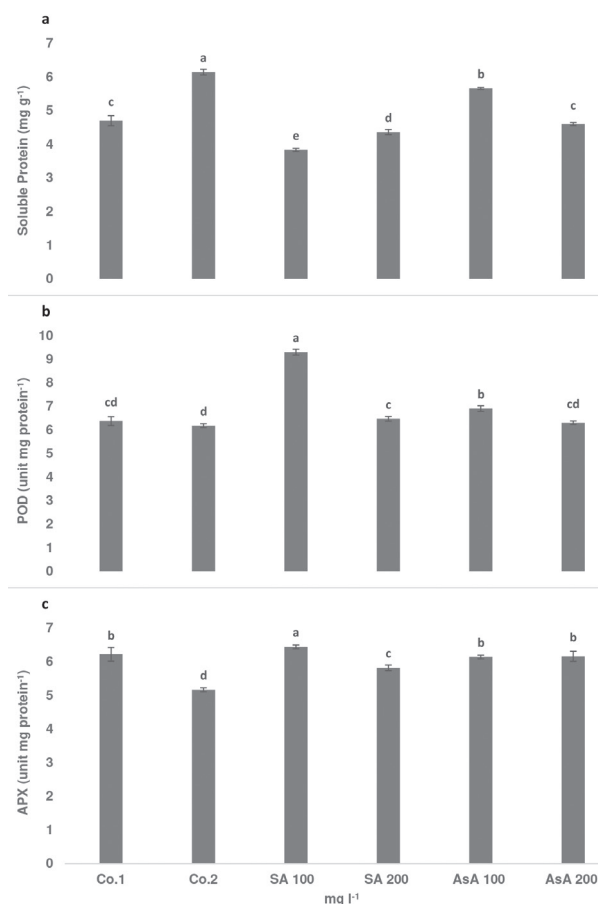


Fig. 2. Effect of salicylic acid (SA) and ascorbic acid (AsA) on soluble protein (a), peroxidase (b), and ascorbate peroxidase (c) of the date palm seedlings growing under the UV-B light stress. Co.1: Control with white light only; Co.2: Control with white light and UV-B light. The averages of 5 samples \pm SD. Columns containing various letters are significantly distinct at $p \leq 0.01$ after the Duncan test.

mechanisms like photosynthesis, osmotic adjustment, and wave signals acting together for growth under stress (ALI et al., 2023). SA might not only enhance its growth-promoting effect by reducing damage caused by reactive oxygen species (SANGWAN et al., 2022) but also modulate signaling pathways for PHSs and activities of antioxidant enzymes. AsA, also known for its antioxidant properties, plays an important role in preserving cellular functions under stress by protecting against oxidation damage and supporting cell division (KHAZAEI et al., 2020).

SA and AsA treatments showed a considerable increase in total chlorophyll content under UV-B stress (photoprotection) (Table 2). This is in accordance with the recommendations that SA can contribute to preventing chlorophyll from oxidative damage (KHALVANDI et al., 2021). Compared to the plants with white light, the plants with the treatment of UV had lower chlorophyll content as a result of oxidative stress from UV radiation that increased the production of ROS, which would cause pigment to be oxidized and subsequently degraded (SWAID et al., 2020). Plants treated with SA and AsA retain chlorophyll in the ploy scale, a relatively common chlorophyll degeneration,

resulted from UV-B-induced oxidative damage, indicating their protective roles (KUMAR et al., 2022).

AsA serves an important role in chlorophyll stability, and it is recognized as a catalyst that replenishes other antioxidants, preventing chlorophyll degradation (ABDULLAH et al., 2023a). Higher and alternative carotenoid and anthocyanin concentration in response to the treatments shows the complex relationship that exists between antioxidant treatments and pigmentation synthesis, which is consistent with plant adaptive response to UV-inducement damage (SHAREEF et al., 2020). Similar results were observed by SWAID et al. (2020a) when date palm seedlings were exposed to high doses of UV-B (8–10 hours). The reduced level of carotenoids associated with high levels of antioxidants, especially in AsA-treated seedlings, may be a reflection of the altered balance of the antioxidants in the plant, with an effective coordination of SA and AsA for oxidation stress management, and hence reduced dependency on proteins in exerting protection.

The reduction of oxidative stress markers as represented by MDA and H₂O₂ in seedlings treated with SA and AsA compared with the control seedlings supports this conclusion (Fig. 1). Such results are consistent with studies stating that the function of antioxidant enzymes, particularly POD and SOD, that are responsible for the elimination of excess reactive oxygen species and protection of cell structures from damage, can be improved by SA treatment (ALAM et al., 2023). However, the stability of enhanced membrane stability in treated seedlings might be a result of the activation of antioxidant defence systems, which include POD and APX that are essential to eliminate reactive types of oxygen and ensure the integrity of cellular systems under stress conditions (HASANUZZAMAN et al., 2021). The significant function of a well-known protective agent for plants, AsA, is confirmed by directly scavenging reactive oxygen species and maintaining cell membrane stability over varying stress durations (BILSKA et al., 2019).

Accordingly, the higher levels of soluble proteins resulting from SA and AsA treatments suggest these antioxidants helped to stabilize proteins or mitigate protein degradation under UV stress (Fig. 2a). Indicating that they might preserve cellular integrity and assist other cell metabolic processes under suboptimal environments. This has been confirmed in several studies, which showed that both SA and AsA increase the expression of proteins and enzymes belonging to the stress responsiveness pathway necessary for maintaining cellular homeostasis under unjust conditions (SHAREEF, 2019; JALILI et al., 2023). In addition to protecting from environmental stress and damage, their role in stabilizing protein from oxidation and turnover values is important (LLAURADÓ MAURY et al., 2020).

An even more significant enhancement in antioxidant enzyme activities, including POD and APX, which is due to the analyzed enzymes confirming that all of them play a vital role in plant defence against oxidation stress (Fig. 2b and c). It is well documented that the induction of SAR upregulates these enzymes and enhances ROS detoxification capacity (YU et al., 2022). Taken together, the ability

of SA and AsA to modulate both enzymatic and non-enzymatic antioxidant systems thus suggests their potential practical usefulness for improving the impaired capability of crops to cope with the increased abiotic stress at higher levels of UV-B radiation.

Conclusion

The present study results indicated that salicylic acid and ascorbic acid treatments improve date palm seedlings' performance by modulating the antioxidant enzyme activities and chlorophyll content, besides enhancing the tolerance level of seedlings against harmful effects of UV-B stress via alleviating oxidative damage. These findings underscore the potential role of external antioxidants in alleviating adverse effects of UV-B stress on crops that may require more flexible agricultural practices.

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