

MORPHOLOGICAL, PHYSIOLOGICAL AND BIOCHEMICAL RESPONSE OF TWO COMMERCIAL DATE PALM CULTIVARS TO INDUCED SALT STRESS

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Abstract

Salinity stress significantly impacts the growth and development of date palm cultivars. This study examines the morphological, physiological, and biochemical traits of two date palm cultivars, Barhi and Khalas, to varying salinity levels (0, 5, and 6 dS m⁻¹), highlighting their adaptive mechanisms and resilience under salt stress conditions. Under non-saline conditions (0 dS m⁻¹), both cultivars exhibited optimal growth, with Barhi showing slightly higher shoot elongation rate, leaf area, leaf growth rate, leaf fresh weight, and root length compared to Khalas. However, as salinity increased, significant reductions in these parameters were observed, with Khalas demonstrating greater tolerance to salinity stress. At 5 dS m⁻¹, Khalas maintained higher shoot elongation rate, leaf area, leaf growth rate, leaf fresh weight, and leaf dry weight compared to Barhi, indicating better adaptation to moderate salinity. Under severe salinity (6 dS m⁻¹), Khalas continued to outperform Barhi, suggesting greater resilience to salt stress. Under non-saline conditions, Barhi exhibited higher chlorophyll content, photosynthetic rate, and stomatal conductance than Khalas. However, as salinity increased, Khalas maintained relatively higher chlorophyll content, photosynthetic rate, and relative water content, indicating better physiological adaptation to salinity. Barhi showed a more pronounced decline in these parameters, reflecting higher sensitivity to salt stress. Biochemical analysis revealed that Khalas accumulated less sodium and hydrogen peroxide under salinity stress compared to Barhi, suggesting better ion homeostasis and oxidative stress management. Proline content increased in both cultivars under salinity, but Barhi exhibited higher proline accumulation, potentially reflecting a less efficient stress response compared to Khalas. This study concluded that Khalas demonstrated superior tolerance to salinity stress across morphological, physiological, and biochemical traits, making it a more suitable cultivar for cultivation in saline environments. These findings provide valuable insights for selecting salt-tolerant date palm cultivars and improving crop resilience in saline-affected regions.

Key words: Date palm cultivars, Salinity stress, Salt tolerance, Oxidative stress, Photosynthesis, Proline, Water use efficiency, Crop resilience.

Introduction

Date palm (*Phoenix dactylifera* L.) cultivation is an important agricultural activity worldwide, especially in arid and semi-arid regions. The Middle East and North Africa (MENA) region dominates global date production, with countries like Egypt, Saudi Arabia, Iran, Algeria, and the United Arab Emirates being major producers (Alotaibi *et al.*, 2023a). Arab countries, particularly those in the Gulf region, have a long history of date farming due to their suitable climate and cultural significance of dates. Date palm cultivation is a vital agricultural sector in Saudi Arabia, playing a significant role in the country's economy, culture, and food security. With over 30 million date palms spread across various regions, Saudi Arabia is one of the world's leading producers and exporters of dates (Al-Karmadi & Okoh, 2024). The government of Saudi Arabia actively supports the date industry through initiatives like research and development programs, quality control measures, and export promotion. Saudi dates, particularly cultivars like Ajwa, Sukkari, and Khalas, are highly sought after in international markets, contributing to the Kingdom's non-oil revenue and reinforcing its agricultural sustainability goals (Aleid *et al.*, 2015; Alumushaiti, 2024).

Salinity is a major environmental challenge affecting soil and water resources worldwide. It occurs when the concentration of soluble salts in soil or water increases to levels that hinder plant growth and agricultural productivity (Majeed & Muhammad, 2019; Adil *et al.*, 2023; Sajid *et al.*, 2023). It results from natural processes such as seawater intrusion, weathering of rocks, and poor drainage, or from human activities like excessive irrigation, improper land management, and the use of saline

water for agriculture. Globally, salinity is a significant issue, particularly in arid and semi-arid regions where evaporation rates are high, causing salts to accumulate in the soil. Countries such as Australia, India, Pakistan, the United States, and parts of the Middle East struggle with salinization, which leads to reduced crop yields, land degradation, and economic losses for farmers (Pitman & Läuchli, 2002; Hopmans *et al.*, 2021).

In Saudi Arabia, salinity poses a critical challenge due to the country's harsh desert climate, limited freshwater resources, and dependence on groundwater for irrigation (Alotaibi *et al.*, 2023a). High evaporation rates and low rainfall contribute to the accumulation of salts in agricultural soils, reducing fertility and affecting crop production. The use of desalinated water and brackish groundwater for irrigation further exacerbates the issue, leading to soil degradation over time (Al-Wabel *et al.*, 2020; Devkota *et al.*, 2022). Date palm plantations, a major agricultural sector in Saudi Arabia, are particularly vulnerable to salinity stress, affecting productivity and quality (Aleid *et al.*, 2015). The government and research institutions in Saudi Arabia are actively working on solutions, including improved irrigation practices, the development of salt-tolerant crops, and soil reclamation techniques. Technologies such as drip irrigation, artificial drainage systems, and soil amendments like gypsum are being explored to mitigate salinity-related problems (Al-Wabel *et al.*, 2020; Alkharabsheh *et al.*, 2021). Addressing salinity is crucial for ensuring sustainable agriculture and food security in the Kingdom, as it seeks to optimize its limited water resources and maintain agricultural productivity in an arid environment (Fiaz *et al.*, 2018, Yusuf *et al.*, 2025).

Salinity is a major abiotic stress affecting date palm cultivation, especially in arid and semi-arid regions where saline irrigation water is commonly used. It impacts date palms at physiological, biochemical, and molecular levels, leading to reduced growth, yield, and fruit quality due to osmotic stress, ion toxicity, and nutrient imbalances that disrupt water uptake, photosynthesis, and metabolism (Al-Absi, 2023; Alotaibi *et al.*, 2023b; Abul-Soad *et al.*, 2023). Excessive sodium and chloride accumulation interferes with potassium and calcium absorption, essential for cellular functions and plant health. However, date palm cultivars vary in salt tolerance, with some exhibiting adaptive mechanisms such as selective ion uptake, osmoprotectant accumulation, and antioxidant enzyme activity. Salinity also affects seed germination, root elongation, and leaf chlorophyll content, reducing productivity and economic value (Al-Omran *et al.*, 2023; Hussain *et al.*, 2024; Du *et al.*, 2025). Molecular studies are increasingly identifying salt-tolerant genes and developing genetically improved cultivars (Al-Khateeb *et al.*, 2020; Hazzouri *et al.*, 2020).

Understanding the physiological and biochemical responses of date palms to salinity is crucial for developing effective mitigation strategies, ensuring sustainable production, and maintaining food security in salt-affected regions, while also identifying and selecting salt-tolerant cultivars that can sustain productivity under challenging conditions. While previous studies have examined salinity tolerance in date palms, there is a need for a comprehensive study that integrates morphological, physiological, and biochemical responses to induced salt stress. Investigating these responses will provide valuable insights into the adaptive mechanisms of different cultivars, contributing to improved management practices and breeding programs. This study focuses on two commercially important date palm cultivars, Khalas and Barhi evaluating their tolerance to salinity through multiple physiological and biochemical indicators.

Material and Methods

Research venue, date palm offshoots selection, and pot media: A two years (2022–2023) glasshouse pot experiment was conducted at the Date Palm Research Center of Excellence, King Faisal University, Kingdom of Saudi Arabia (latitude 25°16'17" N and longitude 49°42'22" E). The arch roof glasshouse is constructed from galvanized iron pipes, columns, beams, and brackets. It has a 136.5 m² ground area and a central point height of 3.5 m. A PCE-THB 40 data logger installed in the glasshouse to record temperature and humidity, and LI190SB-L quantum sensor to measure solar irradiance. The glasshouse's dimensions are 21 m × 6.5 m. Uniform six-year-old offshoots of commercial date palm cultivars Khalas and Barhi were obtained from SAPAD Tissue Culture Date Palm Company, Dammam, Saudi Arabia (latitude 26°29'10" N and longitude 49°58'06" E). These plants were produced through meristem tissue culture technique. Date palm plants were potted (72 L volume, 45 cm diameter, 45.5 cm height) in a 1:2 mixture of sandy loam soil and peat moss compost. The analysis of sandy loam soil indicated that it contained 81.35% sand, 9.88% silt, 8.77% clay, 7.83 pH, 3.63 dS m⁻¹ EC, 4.16% moisture content, 1.48 g cm⁻³ bulk density, 0.27% organic matter, 16.48 mg kg⁻¹ total nitrogen, 9.85 mg kg⁻¹ phosphorus,

11.38 mg kg⁻¹ potassium, and 18.33 mg kg⁻¹ sodium. The peat moss had 5.41 pH, 1.89 dS m⁻¹ EC, 40.37% moisture content, 0.91 g cm⁻³ bulk density, 90.16% organic matter, 892 mg kg⁻¹ total nitrogen, 387 mg kg⁻¹ phosphorus, 4.59 mg kg⁻¹ potassium, and 244 mg kg⁻¹ sodium. The mean diurnal temperature of the glasshouse was 27±2 °C, relative humidity 50±5%, and 14 h day⁻¹ photoperiod (750 μmol m⁻² s⁻¹ photosynthetic photon flux density-PPFD). Environmental conditions within the glasshouse were maintained uniformly for both cultivars during the entire study period. Fertigation was employed to supply nutrients uniformly to both cultivars at scheduled intervals, utilizing a solution with an N:P:K:S ratio of 16:08:16:15.

Salinity stress levels and experiment design: Five plants of date palm cultivars Khalas and Barhi were subjected to 5 and 6 dS m⁻¹ (equivalent to 3200 and 3840 ppm, respectively) sodium chloride (NaCl) salinity levels, excluding the same number of replicates of each cultivar as control (0 dS m⁻¹). Total thirty date palm plants of both cultivars were used in the present study. The experiment was laid out on a two-factorial completely randomized design with five replications of each date palm cultivar. To prepare the NaCl salinity solution, the required amount of NaCl (71387, >99.5%, Merck KGaA, Darmstadt, Germany) was first weighed: 3.2 g for a 5 dS m⁻¹ solution or 3.84 g for a 6 dS m⁻¹ solution. One-liter volumetric flask was taken, and the measured NaCl was added. Distilled water (500 mL) was poured into the flask, and the mixture was stirred using electric shaker (Model: Oxford BenchMate 10 mm-OS-10, Lab Pro Inc., USA) until the salt dissolved completely. Once dissolved, more distilled water was added to bring the total volume to one liter. An electric conductivity (EC) meter (HI-2003 Edge Conductivity Meter, Hanna Instruments Ltd., UK) was used to check the EC of the solution, ensuring it met the desired level of 5 or 6 dS m⁻¹. The solution was stored at 4°C in a clean, tightly sealed flasks to prevent contamination.

Plants selected for salt treatments were irrigated at 100% field capacity every fourth day with a respective salinity level of NaCl, whereas control plants received tap water only. The field capacity of the pots was assessed by fully saturating the soil with water. To minimize evaporation, the pots were covered with plastic sheets and allowed to drain for three days. After this period, their weights were recorded. The soil moisture content at field capacity was then determined by calculating the difference between the soil weight after drainage and the soil weight after being oven-dried at 105°C for 24 hours (Samarah, 2005; Dane & Topp, 2020). After ninety-two days, both morphological and physiological characteristics were assessed. Following the evaluations, the leaves of both date palm cultivars were harvested for biochemical analysis.

Morphological, physiological, and biochemical characteristics: Palm height measurements were taken at the collar level, using the zero-meter mark as a reference point, at the start of the experiment and again after ninety-two days. This approach allowed to calculate the shoot elongation rate. Leaf area was measured using portable laser leaf area meter (CI-203, CID Bio-Science, USA). Leaf growth rate was calculated by measuring the leaf length after ninety-two (L2) minus initial leaf length (L1)

divided by L2, multiplied by hundred. At the end of the experimental period, leaves from each date palm cultivar were collected and weighed to determine their fresh weight. The leaves were then dried in a forced-air ventilated oven at 70°C until a constant weight was achieved, which was recorded as the dry weight. Then the ratio of leaf fresh weight and leaf dry weight was calculated. The roots were cleaned to remove any attached soil, and their lengths were measured.

Leaf chlorophyll content was assessed a day before harvest using the SPAD-502 handheld chlorophyll meter (Konica Minolta Sensing Inc., Japan). Net photosynthesis, stomatal conductance, transpiration rate, and intercellular CO₂ concentration were measured using a portable Li6400XT photosynthesis system, following the methodology described by Iqbal *et al.*, (2022) and Munir *et al.*, (2024). The intrinsic water use efficiency (WUEi) was calculated as the ratio of net photosynthesis to stomatal conductance (Medlyn *et al.*, 2017, Yi *et al.*, 2019), whereas instantaneous water use efficiency (WUEinst) was calculated as the ratio of net photosynthesis to transpiration rate (Medrano *et al.*, 2015; Munir *et al.*, 2020; Iqbal & Munir, 2024).

Relative water contents were estimated after 92 days of treatments as described by Khakwani *et al.*, (2011) and Alhajhoj *et al.*, (2022). Electrolyte leakage was determined at the end of the study according to Sairam & Srivastava, (2002). Fresh leaf samples weighing 0.1 g were incubated in a 100 mL deionized water bath at 40°C for 30 minutes. The electrical conductivity (EC) of the solution was measured using an EC meter (recorded as EC1). The samples were then re-incubated in a water bath at 100°C for 15 minutes, and the EC was measured again (recorded as EC2). The percentage of electrolyte leakage was calculated by dividing EC1 by EC2 and multiplying by 100.

Leaf sodium content was determined using a flame photometer with standard sodium solutions as described by Benaceur *et al.*, (2024). Leaf proline content was determined following the methodology outlined by Bates *et al.*, (1973) and Ali-Dinar *et al.*, (2023). Leaf samples (0.1 g) from each treatment group were homogenized in 3% sulfosalicylic acid, filtered, and added to glacial acetic acid and acidic ninhydrin. The mixture was heated (100°C for 1 h), cooled, and extracted with toluene. The chromophore containing toluene was isolated and its optical density measured at 520 nm. Similarly, to determine H₂O₂ content, fresh leaves were homogenized with 10% trichloroacetic acid, centrifuged at 15,000 rpm for 15 minutes, and the supernatant was collected. The supernatant was then mixed with phosphate buffer, pH 7, and potassium iodate, and the absorbance was measured at 390 nm after 1 hour of incubation in the dark (Velikova *et al.*, 2000; Benaceur *et al.*, 2024).

Statistical analysis

To assess the statistical significance of variations in morphological, physiological, and biochemical traits among different date palm cultivars under salinity stress, analysis of variance (ANOVA) was conducted using Genstat software (14th Edition, VSNi, Hemel Hempstead, England). A post hoc Tukey test was then performed to evaluate significant difference between samples, with a significance threshold set at a probability value of less than 0.05 ($p < 0.05$). The path

coefficient correlation analysis was performed using the R programming scripts (R 4.4.2, R Core Development Team, Vienna). The post hoc pairwise tests of independence in conjunction with asymptotic generalized Pearson chi-squared tests were used to assess any association between the frequencies of morpho-physiological and biochemical parameter. Boxplot, correlation, chord diagrams, and principal components analysis (PCA) were generated using RStudio 2024-12.1+563.pro5 (Posit Software, MA, USA), integrated into the R software, visualization of 'boxplot', 'corrplot', 'circlize', and 'ggplot' packages.

Results

Morphological characteristics: The boxplot illustrates the effect of varying salinity levels (0, 5, and 6 dS m⁻¹) on the shoot elongation rate (SER), leaf area (LA), leaf growth rate (LGR), leaf fresh weight (LFW), leaf dry weight (LDW), leaf fresh weight to leaf dry weight ratio (LFW:LDW), root length (RL) of two date palm cultivars, Barhi and Khalas (Fig. 1). Under non-saline conditions (0 dS m⁻¹), both cultivars exhibit the significantly highest SER, with Barhi showing a slightly greater SER (8.99 cm) than Khalas (8.08 cm) (Fig. 1A). However, as salinity increases, a significant reduction in SER is observed across both cultivars, indicating the adverse effects of salinity stress on plant growth. At 5 dS m⁻¹, Khalas maintains a relatively higher SER (5.16 cm) than Barhi (3.63 cm), suggesting a greater tolerance to moderate salinity. Under severe salinity stress (6 dS m⁻¹), SER is further inhibited, with Khalas still exhibiting a slightly higher SER (3.42 cm) than Barhi (1.50 cm). Fig. 1B shows that under control conditions (0 dS m⁻¹), both cultivars exhibit the highest LA, with minimal variability (31.90–33.03 cm²). As salinity increases to 5 dS m⁻¹, a significant reduction in LA is observed in both cultivars, though Khalas maintains a slightly larger LA (23.98 cm²) than Barhi (18.22 cm²), suggesting a better adaptive response. At 6 dS m⁻¹, LA declines further, with Khalas still exhibiting a marginally higher LA (17.48 cm²) compared to Barhi (11.81 cm²). Under control conditions (0 dS m⁻¹), both cultivars exhibit the highest LGR, with Barhi showing a slightly greater (26.89) than Khalas (25.50) (Fig. 1C). As salinity increases to 5 dS m⁻¹, there is a noticeable decline in LGR in both cultivars; however, Khalas maintains a higher growth rate (18.31) than Barhi (15.51), suggesting a comparatively better tolerance to moderate salinity stress. At the highest salinity level (6 dS m⁻¹), LGR drops significantly in both cultivars, with Khalas still exhibiting a marginally higher growth rate (13.63) than Barhi (9.83), indicating some level of resilience. Under non-saline conditions (0 dS m⁻¹), both cultivars exhibit the highest LFW, with Barhi showing slightly greater values (44.72 g) than Khalas (42.98 g), suggesting an inherently higher biomass production potential (Fig. 1D). As salinity increases to 5 dS m⁻¹, a substantial reduction in LFW is observed in both cultivars; however, Khalas maintains a higher LFW (35.50 g) than Barhi (30.88 g), indicating a relatively better tolerance to moderate salinity stress. At the highest salinity level (6 dS m⁻¹), both cultivars show a further decline in LFW, with Khalas still performing slightly better (27.89 g) than Barhi (22.71 g). The boxplot in Fig. 1E demonstrates that under non-saline conditions (0 dS m⁻¹), both cultivars exhibit the highest LDW, with Barhi showing slightly higher values (26.95 g) and greater variability than Khalas ((25.40 g),

indicating a potential difference in structural biomass accumulation. As salinity increases to 5 dS m⁻¹, a significant reduction in LDW is observed in both cultivars, with Khalas maintaining a higher LDW (18.17 g) than Barhi (14.94 g), suggesting a better ability to sustain biomass production under moderate salinity stress. At the highest salinity level (6 dS m⁻¹), both cultivars experience a further reduction in LDW, with Khalas still exhibiting a slightly higher (13.78 g) over Barhi (9.55 g). Fig. 1F shows that both cultivars under control conditions (0 dS m⁻¹) exhibit the lowest LFW:LDW ratios. As salinity increases (5 dS m⁻¹), the LFW:LDW ratio rises in both cultivars (1.72–1.66), indicating higher water retention relative to dry biomass under moderate salinity stress. Notably, Barhi at 5 dS m⁻¹ demonstrates a greater increase in LFW:LDW ratio (2.07) compared to Khalas (1.96), suggesting a differential osmotic adjustment strategy between the cultivars. At 6 dS m⁻¹, Barhi continues to exhibit the highest LFW:LDW ratio (2.38), which may reflect higher water accumulation or reduced structural biomass investment under severe salinity stress. Khalas, however, shows a comparatively lower increase in the ratio (2.02) at 6 dS m⁻¹, which could indicate a better balance between water retention and dry matter accumulation, potentially contributing to greater stress resilience. Under control conditions (0 dS m⁻¹), Barhi exhibits the longest root length (97.37 cm), followed by Khalas (85.55 cm), indicating an inherent genetic difference in root system development in both cultivars (Fig. 1G). As salinity increases (5 dS m⁻¹), a significant reduction in root length is observed in both cultivars, with Barhi (58.56 cm) experiencing a greater reduction compared to Khalas (69.90 cm), suggesting that Barhi may be more sensitive to moderate salinity stress in terms of root elongation. At the highest salinity level (6 dS m⁻¹), both cultivars show a further decline in root length, with Barhi (44.41 cm) exhibiting a more pronounced reduction than Khalas (54.78 cm).

Physiological characteristics: Under non-saline conditions (0 dS m⁻¹), Barhi exhibited the highest CC (68.20 SPAD), followed by Khalas (64.26 SPAD), indicating better initial chlorophyll retention in Barhi (Fig. 2A). As salinity increased (5 dS m⁻¹), both cultivars showed a decline in CC, though Khalas maintained relatively higher (58.90 SPAD) than Barhi (53.52 SPAD). At the highest salinity level (6 dS m⁻¹), CC further declined, with Barhi showing the most substantial reduction (45.01 SPAD) than Khalas (52.82 SPAD), as evidenced by the lower median and wider variability. Fig. 2B shows that both cultivars grown under non-saline conditions (0 dS m⁻¹), exhibited high *Pn*, with Barhi displaying a slightly higher median value (12.38 $\mu\text{mol m}^{-2} \text{s}^{-1}$) compared to Khalas (11.83 $\mu\text{mol m}^{-2} \text{s}^{-1}$). As salinity increased to 5 dS m⁻¹, there was a significant reduction in photosynthesis for both cultivars, with Barhi experiencing a more pronounced decline (8.03 $\mu\text{mol m}^{-2} \text{s}^{-1}$). However, Khalas maintained a relatively higher median *Pn* under moderate salinity (10.07 $\mu\text{mol m}^{-2} \text{s}^{-1}$). At the highest salinity level (6 dS m⁻¹), *Pn* further decreased in both cultivars, with Barhi showing the lowest median value and greater variability (6.39 $\mu\text{mol m}^{-2} \text{s}^{-1}$), suggesting a higher sensitivity to salinity stress. In contrast, Khalas demonstrated a more stable *Pn* response under increasing salinity, indicating a greater tolerance to salinity-induced stress (7.79 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Under non-saline conditions (0 dS m⁻¹), Barhi exhibited the highest *gs* (66.33 mmol m⁻² s⁻¹),

followed by Khalas (63.20 mmol m⁻² s⁻¹), suggesting greater gas exchange capacity in Barhi under optimal conditions (Fig. 2C). As salinity increased to 5 dS m⁻¹, both cultivars experienced a notable decline in *gs*, with Barhi showing a more pronounced reduction (39.34 mmol m⁻² s⁻¹) compared to Khalas (44.03 mmol m⁻² s⁻¹). At the highest salinity level (6 dS m⁻¹), *gs* further decreased, with Barhi exhibiting the lowest median value and greater variability (30.00 mmol m⁻² s⁻¹), indicating a stronger sensitivity to salinity stress. Khalas, in contrast, maintained relatively higher *gs* (37.74 mmol m⁻² s⁻¹) under both moderate and severe salinity conditions. Under non-saline conditions (0 dS m⁻¹), both cultivars exhibited the highest *E*, with Barhi displaying slightly greater values (1.71 $\mu\text{mol mol}^{-1}$) than Khalas (1.66 $\mu\text{mol mol}^{-1}$) (Fig. 2D). As salinity increased to 5 dS m⁻¹, a notable decline in *E* observed in both cultivars, though Khalas maintained a higher rate (1.43 $\mu\text{mol mol}^{-1}$) compared to Barhi (1.29 $\mu\text{mol mol}^{-1}$). At the highest salinity level (6 dS m⁻¹), *E* further decreased, with Barhi showing a more pronounced reduction (0.80 $\mu\text{mol mol}^{-1}$) than Khalas (1.11 $\mu\text{mol mol}^{-1}$). Under non-saline conditions (0 dS m⁻¹), both cultivars exhibited the highest *Ci*, with Barhi showing slightly greater values (377.06 mmol m⁻² s⁻¹) than Khalas (359.25 mmol m⁻² s⁻¹) (Fig. 2E). As salinity increased to 5 dS m⁻¹, a substantial decline in *Ci* was observed in both cultivars, though Khalas maintained higher values (308.02 mmol m⁻² s⁻¹) compared to Barhi (282.74 mmol m⁻² s⁻¹). At the highest salinity level (6 dS m⁻¹), a further reduction was evident, with Barhi exhibiting a more pronounced decline (246.58 mmol m⁻² s⁻¹) than Khalas (285.35 mmol m⁻² s⁻¹). Under control conditions (0 dS m⁻¹), both cultivars maintained high RWC, with Barhi exhibiting slightly higher values (85.39) than Khalas (82.41) (Fig. 2F). As salinity increased to 5 dS m⁻¹, a significant decline in RWC was observed in Barhi (66.89), whereas Khalas exhibited a relatively smaller reduction (73.74), suggesting a better water retention capacity. At the highest salinity level (6 dS m⁻¹), both cultivars showed further reductions in RWC, with Barhi experiencing a more pronounced decrease (61.74) compared to Khalas (66.78). The boxplot summarizes the WUE_i across varying salinity treatments and two date palm cultivars, Barhi and Khalas (Fig. 2G). A clear divergence in WUE_i is observed between the cultivars, with Barhi demonstrating a considerably higher median WUE_i than Khalas across all salinity levels. Under non-saline conditions (0 dS m⁻¹), both Khalas (7.11) and Barhi (7.26) exhibited similar values, suggesting no significant difference in their performance. As salinity increased to 5 dS m⁻¹, Khalas maintained a relatively stable value (7.06), whereas Barhi experienced a noticeable decline (6.19), indicating a greater sensitivity to salinity stress. At the highest salinity level (6 dS m⁻¹), Khalas showed a slight decrease (6.98), while Barhi exhibited the highest recorded value (8.02), suggesting a potential adaptive response. Fig. 2H represents non-significant variation regarding the WUE_{inst} across different salinity levels and cultivars (Barhi and Khalas). Under non-saline conditions (0 dS m⁻¹), both Khalas and Barhi (0.19 each) exhibited the lowest WUE_{inst} values. As salinity increased to 5 dS m⁻¹, WUE_{inst} showed a notable increase in both cultivars, with Khalas (0.23) displaying a higher value than Barhi (0.20). At the highest salinity level (6 dS m⁻¹), WUE_{inst} continued to rise significantly, reaching 0.21 in Khalas and 0.22 in Barhi.

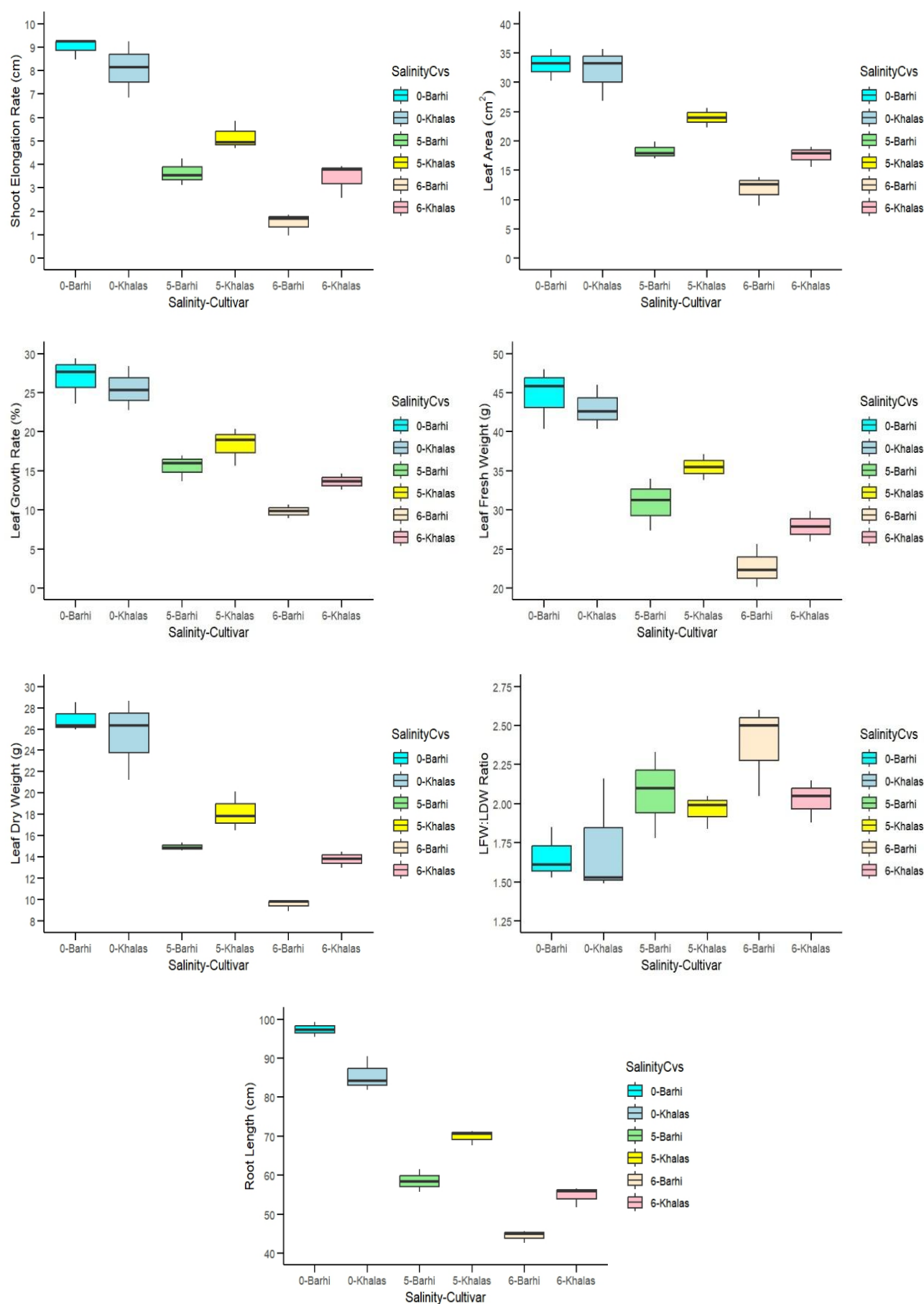


Fig. 1. Morphological characteristics of date palm cultivars Barhi and Khalas subjected to different salinity levels (0, 5, and 6 dS m⁻¹) based on the median index of each factor combination.

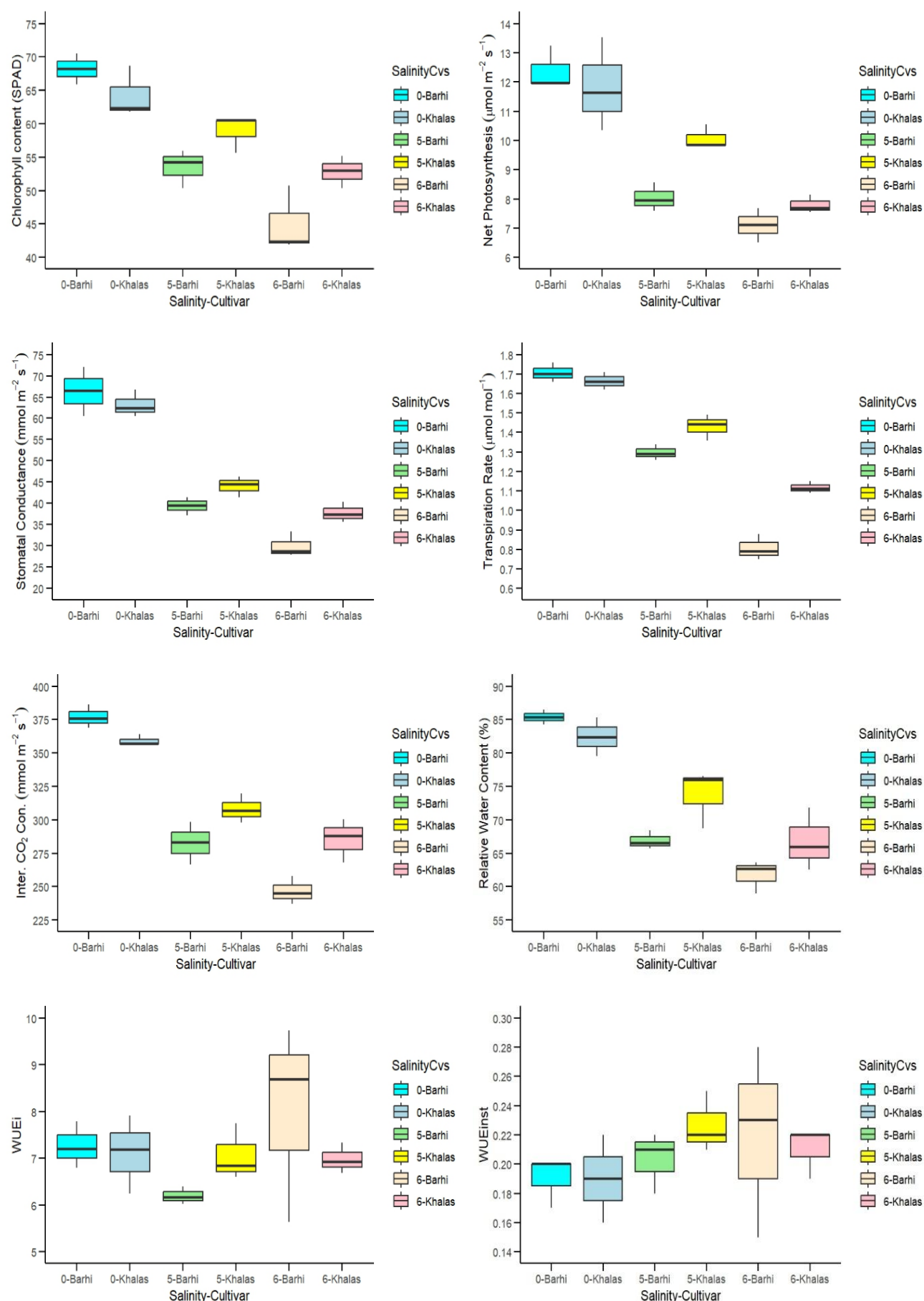


Fig. 2. Physiological characteristics of date palm cultivars Barhi and Khalas subjected to different salinity levels (0, 5, and 6 dS m⁻¹) based on the median index of each factor combination.

Biochemical characteristics: The data in Fig. 3A illustrate the at control (0 dS m⁻¹), both Khalas (12.92 mg g⁻¹ DW) and Barhi (12.63 mg g⁻¹ DW) exhibited the lowest EL values, with no significant difference between them, indicating similar membrane stability in optimal conditions. As salinity increased to 5 dS m⁻¹, EL rose significantly in both cultivars, with Khalas (20.37 mg g⁻¹ DW) displaying a lower EL than Barhi (25.20 mg g⁻¹ DW), suggesting that Barhi experienced greater membrane damage at moderate salinity. At the highest salinity level (6 dS m⁻¹), EL further increased, reaching 24.35 mg g⁻¹ DW in Khalas and peaking at 33.54 mg g⁻¹ DW in Barhi, indicating severe membrane destabilization under extreme salinity stress. At the control level (0 dS m⁻¹), both cultivars maintain low and similar sodium concentrations, Barhi 5.49 and Khalas 5.31 mg g⁻¹ DW (Fig. 3B). However, with increasing salinity, a clear difference in sodium accumulation emerges. Khalas exhibits a lower sodium accumulation in leaves (10.78 and 13.08 mg g⁻¹ DW at 5 and 6 dS m⁻¹, respectively) compared to Barhi (12.62 and 15.07 mg g⁻¹ DW at 5 and 6 dS m⁻¹, respectively). Fig. 3C indicates that plants subjected to non-saline conditions (0 dS m⁻¹), both cultivars maintain low proline content, i.e., 0.60 (Khalas) and 0.65 µg g⁻¹ FW (Barhi). However, with increasing salinity at 5 and 6 dS m⁻¹, Barhi leaves accumulates higher proline content (2.81 and 4.06 µg g⁻¹ FW, respectively) compared to Khalas (2.42 and 3.83 µg g⁻¹ FW, respectively). Under non-saline conditions (0 dS m⁻¹), both cultivars maintain low and comparable H₂O₂ levels, Khalas 3.52 Barhi and 3.82 µg g⁻¹ FW (Fig. 3D). However, Barhi demonstrates a more significant increase in H₂O₂ concentration (16.81 and 25.44 µg g⁻¹ FW) compared to Khalas (13.47 and 19.48 µg g⁻¹ FW) across both salinity treatments (5 and 6 dS m⁻¹).

Path coefficient correlation matrix in Fig. 4 illustrates the relationships between various morphological, physiological, and biochemical traits of date palm cultivars Barhi and Khalas under salinity stress. The hierarchical clustering categorized the correlation data into two main groups. In group one, a strong positive correlation ($r^2 > 0.90$) was observed among traits related to morpho-physiological traits such as SER, LA, LGR, LFW, LDW, RL, CC, *Pn*, *gs*, *E*, *Ci*, and RWC, whereas in second group, a strong positive correlation ($r^2 > 0.90$) was observed among biochemical traits such as EL, LP, HP, and LS. A strong negative correlation existed between both hierarchical groups, which suggests that an increase in oxidative stress leads to impaired physiological functions and reduced plant growth. WUEi and WUEinst showed a moderate positive correlation ($r^2 = 0.73$), indicating they are related but not identical. Both parameters are negatively correlated with most growth and physiological parameters, such as *gs*, *E*, and LA, suggesting that higher WUE is associated with reduced growth and physiological activity. However, WUEinst exhibits stronger negative correlations (e.g., $r^2 = -0.47$ with CC, $r^2 = -0.48$ with *gs*) compared to WUEi. Weak positive correlations with parameters like EL and LP imply some alignment with efficiency in certain biological processes. The correlation analysis highlights the interdependence between water status, photosynthesis, and oxidative stress under salinity stress. Traits associated with higher water retention, stomatal function, and chlorophyll content positively influence plant growth and photosynthesis, whereas increased oxidative stress markers negatively impact these processes. Understanding these interactions is essential for selecting salinity-tolerant genotypes that can maintain high water use efficiency while minimizing oxidative damage, ultimately contributing to improved stress resilience in plants.

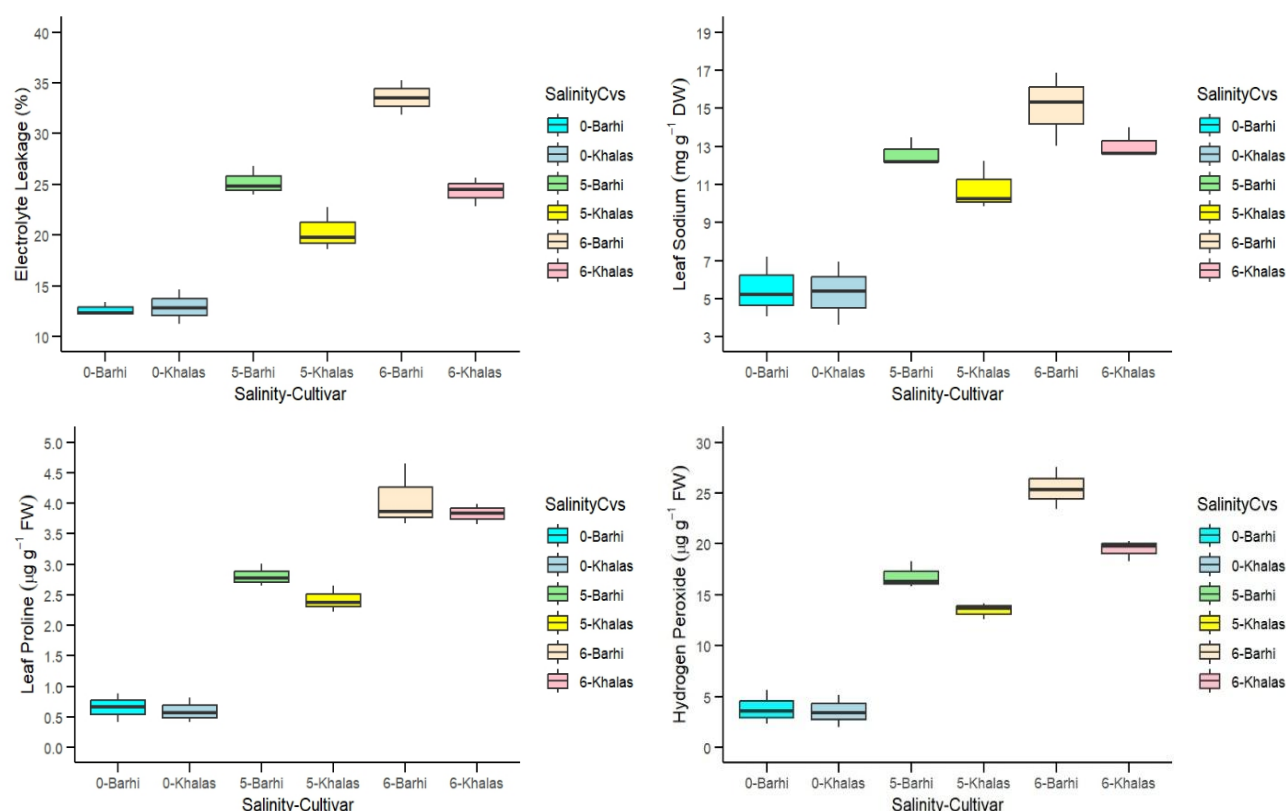


Fig. 3. Biochemical characteristics of date palm cultivars Barhi and Khalas subjected to different salinity levels (0, 5, and 6 dS m⁻¹) based on the median index of each factor combination.

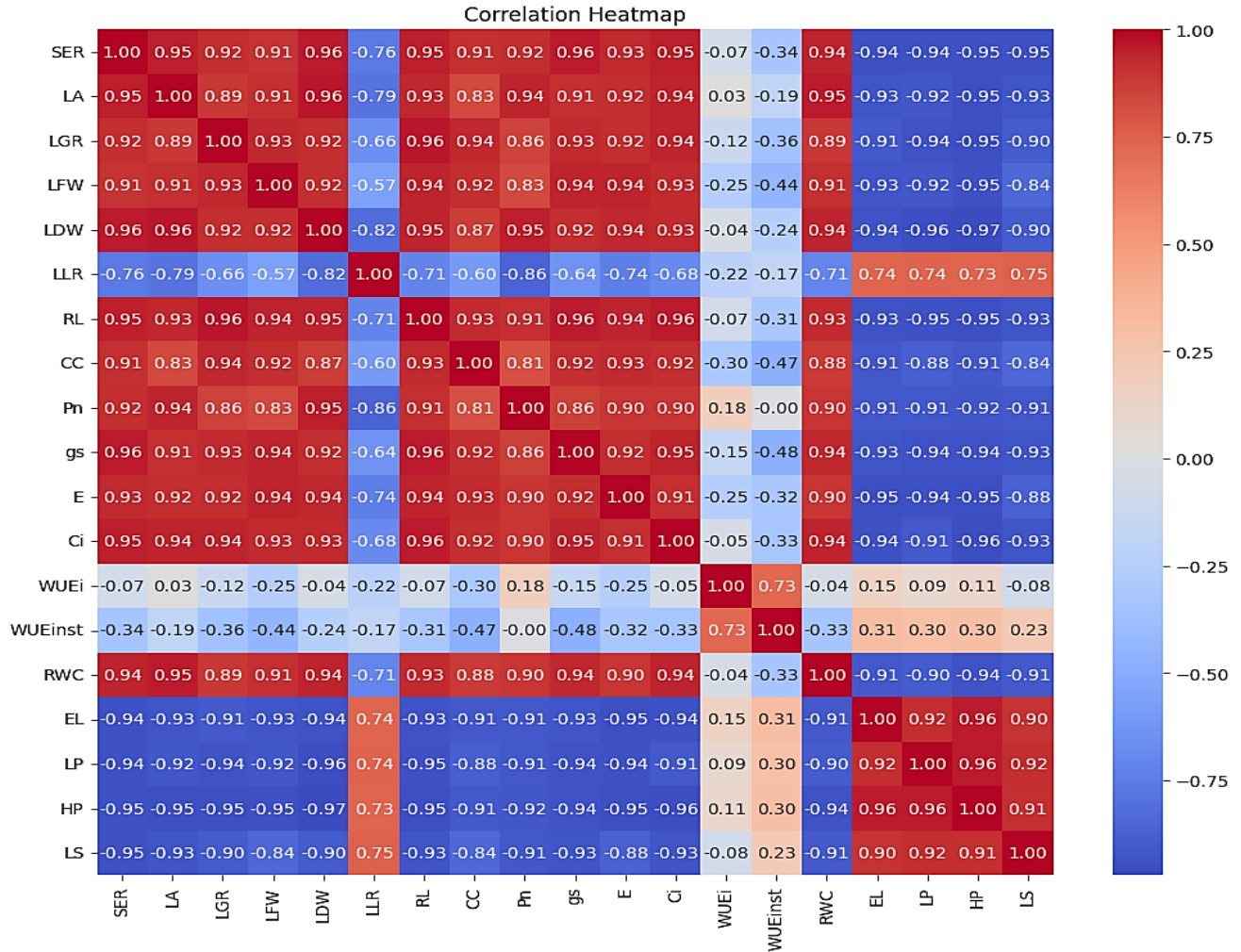


Fig. 4. Correlation heatmap matrix of morpho-physiological and biochemical variables of date palm cultivars (Barhi and Khalas) subjected to salt-stress levels (0, 5, and 6 dS m⁻¹) computed by Pearson-method. These variables are: stem elongation rate (SER), leaf area (LA), leaf growth rate (LGR), leaf fresh weight (LFW), leaf dry weight (LDW), leaf fresh weight to leaf dry weight ratio (LLR), root length (RL), chlorophyll content (CC), net photosynthesis (*Pn*), stomatal conductance (*gs*), transpiration rate (*E*), intercellular CO₂ concentration (*Ci*), intrinsic water use efficiency (WUEi), instantaneous water use efficiency (WUEinst), relative water content (RWC), electrolyte leakage (EL), leaf proline (LP), hydrogen peroxide (HP), and leaf sodium (LS).

The chord diagram indicates that increasing salinity levels had a negative association with SER, LA, LGR, LFW, LDW, RL, CC, *Pn*, *gs*, *E*, RWC, and *Ci* variables, suggesting increased oxidative stress under salinity conditions, while LLR, WUEi, WUEinst, EL, EL, LS, LP, and HP showed a positive association, suggesting a compensatory adaptation under salinity stress (Fig. 5A). A significant association was found between different salinity levels with LA ($\chi^2 = 7.16$; $p = 0.0321$), LGR ($\chi^2 = 5.88$; $p = 0.0455$), LDW ($\chi^2 = 6.01$; $p = 0.0445$), RL ($\chi^2 = 13.19$; $p = 0.0001$), *gs* ($\chi^2 = 11.03$; $p = 0.0001$), *Ci* ($\chi^2 = 17.86$; $p = 0.0001$), EL ($\chi^2 = 6.20$; $p = 0.0445$), and HP ($\chi^2 = 13.04$; $p = 0.0001$). However, a non-significant association was observed between different salinity levels with SER ($\chi^2 = 3.75$; $p = 0.1511$), LFW ($\chi^2 = 5.08$; $p = 0.0778$), LLR ($\chi^2 = 0.07$; $p = 0.8771$), CC ($\chi^2 = 2.65$; $p = 0.2714$), *Pn* ($\chi^2 = 1.36$; $p = 0.5111$), *E* ($\chi^2 = 0.20$; $p = 0.9121$), RWC ($\chi^2 = 2.78$; $p = 0.2524$), WUEi ($\chi^2 = 0.06$; $p = 0.9671$), WUEinst ($\chi^2 = 0.01$; $p = 0.9941$), LS ($\chi^2 = 3.87$; $p = 0.1412$), and LP ($\chi^2 = 2.33.16$; $p = 0.3112$). The Chi-squared test revealed non-significant association between date palm cultivars and all the measured morpho-physiological and biochemical parameters,

which was further supported by a non-significant t-test result (Fig. 5B). This lack of association suggests that the tested parameters do not vary systematically across the different cultivars. The chord diagram represents these weak relationships, highlighting minimal interconnectedness between the groups. This could occur if the cultivars share similar salt-tolerance mechanisms, the salinity levels applied were insufficient to trigger differential responses, or the measured parameters were similarly affected across cultivars. On the other hand, Fig. 5C shows a significant association of salinity levels \times cultivars with LA ($\chi^2 = 15.78$; $p = 0.0075$), LGR ($\chi^2 = 12.42$; $p = 0.0295$), LFW ($\chi^2 = 10.91$; $p = 0.0531$), LDW ($\chi^2 = 12.87$; $p = 0.0246$), RL ($\chi^2 = 29.13$; $p = 0.0001$), *gs* ($\chi^2 = 23.05$; $p = 0.0003$), *Ci* ($\chi^2 = 39.70$; $p = 0.0001$), EL ($\chi^2 = 14.90$; $p = 0.0108$), and HP ($\chi^2 = 27.80$; $p = 0.0001$). However, a non-significant association was observed with SER ($\chi^2 = 8.18$; $p = 0.1467$), LLR ($\chi^2 = 0.17$; $p = 0.9994$), CC ($\chi^2 = 6.22$; $p = 0.2858$), *Pn* ($\chi^2 = 3.05$; $p = 0.6915$), *E* ($\chi^2 = 0.45$; $p = 0.9940$), RWC ($\chi^2 = 6.11$; $p = 0.2953$), WUEi ($\chi^2 = 0.24$; $p = 0.9986$), WUEinst ($\chi^2 = 0.01$; $p = 1.0000$), LS ($\chi^2 = 8.09$; $p = 0.1514$), and LP ($\chi^2 = 4.70.16$; $p = 0.4535$).

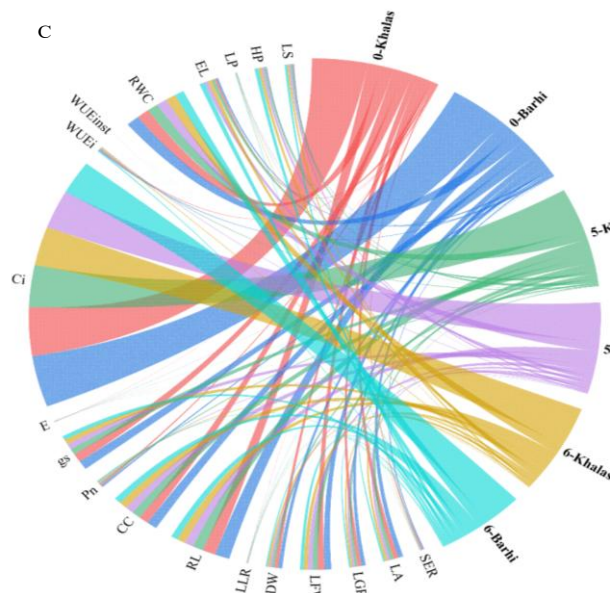
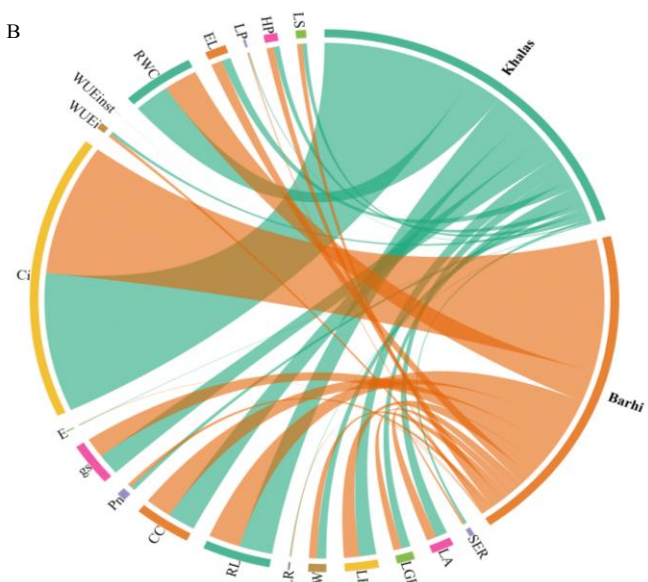
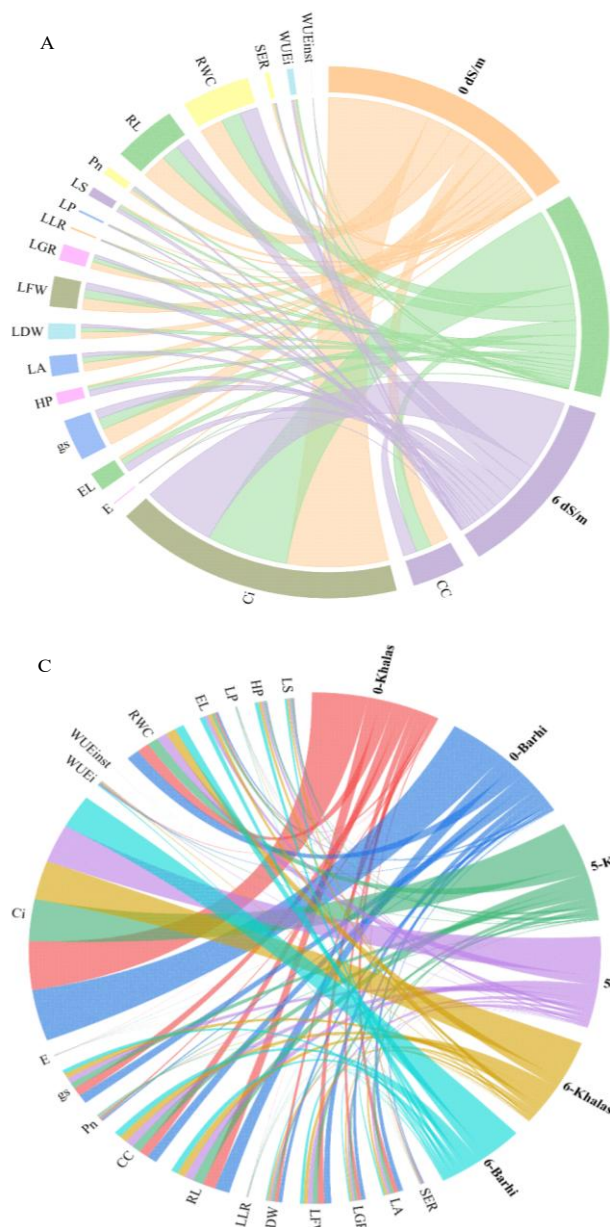


Fig. 5. Chord diagrams showing the association between the different morpho-physiological and biochemical attributes of date palm with (A) salinity levels (0, 5, and 6 dS m⁻¹), (B) cultivars (Barhi and Khalas), and (C) combination of salinity levels × cultivars. The chords are unidirectional whereas the chord thickness corresponds to the observed values of different attributes that is related to respective salinity levels. Morpho-physiological and biochemical variables: stem elongation rate (SER), leaf area (LA), leaf growth rate (LGR), leaf fresh weight (LFW), leaf dry weight (LDW), leaf fresh weight to leaf dry weight ratio (LLR), root length (RL), chlorophyll content (CC), net photosynthesis (*Pn*), stomatal conductance (*gs*), transpiration rate (*E*), intercellular CO₂ concentration (*Ci*), intrinsic water use efficiency (WUEi), instantaneous water use efficiency (WUEinst), electrolyte leakage (EL), leaf sodium (LS), relative water content (RWC), leaf proline (LP), and hydrogen peroxide (HP).

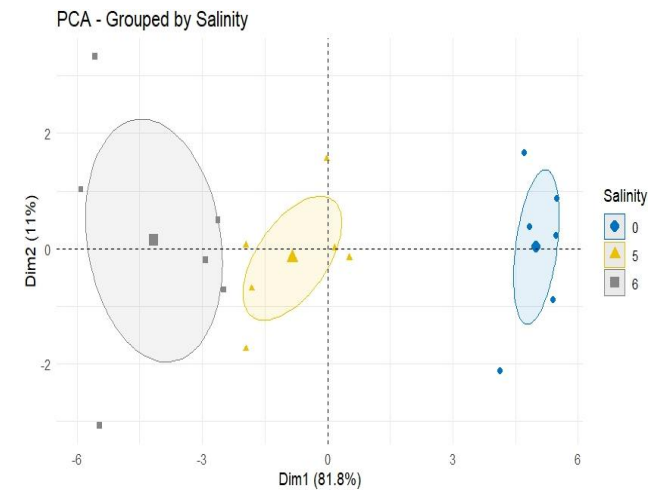
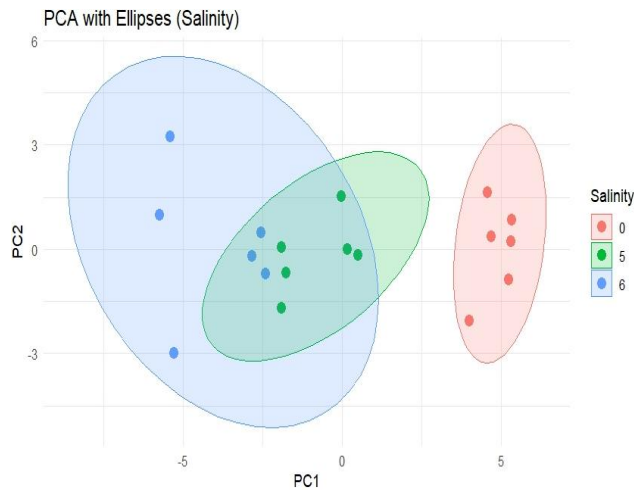


Fig. 6. Principal Component Analysis (PCA) plot with confidence ellipses, grouped by salinity levels (0, 5, and 6 dS m⁻¹). The axes represent the first two principal components (PC1 and PC2), showing the distribution and clustering of data points across different salinity conditions.

Fig. 7. Principal Component Analysis (PCA) plot grouped by salinity levels (0, 5, and 6 dS m⁻¹), illustrating the variance explained by Dim1 (81.8%) and Dim2 (11%). The data points are distributed across different salinity categories, highlighting potential patterns/clusters associated with salinity gradients.

The PCA Figs. 6 and 7 highlight key trends and patterns of various morpho-physiological and biochemical variables affected by salinity levels (0, 5, and 6 dS m⁻¹). Dim 1 (PC1) captures the majority of variance (81.8%), representing the primary axis of variation, while Dim 2 (PC2) accounts for a smaller portion (11%), capturing secondary patterns. The Fig. 6 with ellipses emphasizes the spread and clustering of salinity levels (0, 5, and 6 dS m⁻¹) showing distinct groupings and confidence intervals. The Fig. 7, grouped by salinity, further reinforces these trends by differentiating the positions of salinity levels along Dim 1, indicating significant differences in their contributions to the overall variance. Both figures demonstrate distinct behaviours among salinity levels, with 0 dS m⁻¹ potentially representing a baseline or control condition, while levels 5 and 6 dS m⁻¹ show progressively greater negative deviations, suggesting an increasing variability due to the influence of salt stress. The consistent separation along Dim 1 underscores the dominant role of salinity in driving the variables. The multivariate analysis reveals a clear trend of increasing differentiation among salinity levels, with higher salinity levels (5 and 6 dS m⁻¹) showing more pronounced negative deviations from the baseline (0 dS m⁻¹) likely reflecting underlying salt stress impact.

Discussion

The ability of plants to endure and adapt to salt stress is governed by a complex interplay of various physiological, biochemical, and molecular responses, which determine their resilience (Xiao & Zhou, 2022; Colin *et al.*, 2023; Imran *et al.*, 2024). Despite the severe effect of high salinity levels on different date palm cultivars, some varieties showed better tolerance due to their unique physiological and molecular adaptations. Understanding the complex interplay of physiological, biochemical, and molecular responses is crucial for improving the ability of date palm cultivars to withstand high salinity levels (Al-Busaidi *et al.*, 2022; Benaceur *et al.*, 2024). In the present study, the effect of high salinity levels on date palm cultivars Barhi and Khalas was generally severe, as it disrupted their morphological, physiological, and biochemical characteristics. Under non-saline conditions (0 dS m⁻¹), both date palm cultivars exhibit optimal growth and physiological performance, with Barhi often showing slightly higher values in parameters such as SER, LA, LGR, LFW, LDW, and RL. However, as salinity increases, significant reductions in these parameters are observed in both cultivars, with Khalas consistently demonstrating greater resilience to salinity stress. At moderate (5 dS m⁻¹) and high salinity (6 dS m⁻¹), Khalas maintains a higher SER, LA, LGR, LFW, LDW, and RL compared to Barhi. These findings suggest that Khalas has a greater potential to maintain growth and biomass production under salinity stress, likely due to better osmotic adjustment, ion exclusion mechanisms, and stress-responsive physiological adaptations (Munns & Tester, 2008; Chen & Jiang, 2010; El Rabey, 2019; Benaceur *et al.*, 2024).

The reduction in morphological parameters under salinity stress can be attributed to the adverse effects of osmotic and ionic stress (Arif *et al.*, 2020; Ji *et al.*, 2022). Ionic stress from salinity leads to a significant increase in Na⁺ and Cl⁻ ions in plant tissues, which disrupts ion homeostasis and causes toxicity symptoms such as chlorosis and necrosis in leaves (Balasubramaniam *et al.*, 2023). Salinity limits water uptake, reduces turgor pressure required for cell expansion, and disrupts nutrient uptake, leading to inhibited growth and biomass accumulation (AbdElgawad *et al.*, 2016; Garcia *et al.*, 2019; Riseh *et al.*, 2021). The ability of Khalas to maintain higher morphological traits under salinity stress suggests that it has more efficient mechanisms for coping with these challenges. For example, Khalas may have superior osmotic adjustment capabilities, allowing it to maintain cell turgor and continue growth under conditions of reduced water availability. Additionally, Khalas may possess more effective ion exclusion mechanisms, preventing the toxic accumulation of Na⁺ and Cl⁻ ions in its tissues, which can disrupt cellular functions and inhibit growth (Yaish & Kumar, 2015; Balasubramaniam *et al.*, 2023). Furthermore, the ability of Khalas to maintain higher RL under salinity stress compared to Barhi suggests that it has a more robust root system that can better withstand the salinity stress (Shelden and Munns, 2023). A well-developed root system is critical for water and nutrient uptake, and Khalas has longer roots under salinity stress may contribute to its overall greater resilience (Rewald *et al.*, 2013; Dinnyen, 2019).

In addition to morphological parameters, physiological responses such as CC, Pn, gs, E, and RWC also show significant variation between the two cultivars under salinity stress. These physiological traits were higher in Barhi when grown under non-saline conditions compared to Khalas, suggesting that Barhi has slightly better photosynthetic efficiency under optimal conditions. However, as salinity increases, these traits decline significantly in both cultivars, with Khalas maintaining higher values under moderate (5 dS m⁻¹) and severe (6 dS m⁻¹) salinity stress compared to Barhi. These results indicate that Khalas has a greater capacity to maintain photosynthetic efficiency under salinity stress, likely due to better protection of the photosynthetic machinery and more efficient stomatal regulation (Pan *et al.*, 2021; Zahra *et al.*, 2022). Similarly, as salinity increases, both gs and RWC decline significantly, with Khalas maintaining higher values under moderate and severe salinity stress. These findings suggest that Khalas has better water use efficiency and stomatal regulation under salinity stress, allowing it to maintain higher rates of gas exchange and water retention compared to Barhi (Yaish & Kumar, 2015). In a study by Al-Dakheel *et al.*, (2022), eighteen mature fruit-bearing date palm varieties were assessed under salt stress conditions, revealing significant differences in yield across cultivars. They found that Lulu and Barhi exhibited high salinity tolerance (up to 12 dS m⁻¹), while varieties Fardh and Um Al Hamam demonstrated moderate tolerance (9 dS m⁻¹). In contrast, Shagri and Khnizi were classified as low-tolerance varieties (8 dS m⁻¹).

Present study reveals distinct salinity response strategies between date palm cultivars, driven by divergent physiological mechanisms. Khalas maintained stable WUE_i across salinity levels, indicating effective osmotic adjustment through compatible solute accumulation that preserved photosynthetic gas exchange (Chen *et al.*, 2010; Liao *et al.*, 2022). In contrast, Barhi exhibited critical sensitivity at 5 dS m⁻¹, likely due to Na⁺-induced metabolic disruption, followed by compensatory acclimation at 6 dS m⁻¹ likely due to enhanced K⁺ retention and antioxidant upregulation that optimized carbon assimilation (Shetty *et al.*, 2019). However, WUE_{inst} remained uniformly low and invariant across cultivars and salinity levels, likely atmospheric vapor pressure deficit (VPD) dominated transpiration dynamics (Dindarlou *et al.*, 2019; Hatfield & Dold, 2019). The VPD-driven decoupling might mask salinity effects at the whole-plant level, reducing WUE_{inst} by 97–98% relative to WUE_i. Consequently, while Khalas demonstrates constitutive salinity tolerance, Barhi's plasticity suggests dynamic stress resilience—highlighting genotype-specific adaptations critical for arid-zone cultivation where ionic stress and evaporative demand interact.

Biochemical parameters such as EL, Na⁺ accumulation, LP, and HP levels also provide insights into the differential responses of the two cultivars to salinity stress. Under non-saline conditions, both cultivars exhibit low EL, Na⁺ accumulation, LP, and HP levels, with no significant differences between them. However, as salinity increases, significant increases in these parameters, with Barhi generally showing higher values compared to Khalas. These results suggest that Barhi experiences greater membrane damage (Guo *et al.*, 2019), Na⁺ toxicity (Meir *et al.*, 2014), and oxidative stress (Tanou *et al.*, 2012) under salinity stress compared to Khalas, which may contribute to its reduced growth and physiological performance. Membrane damage is primarily due to the accumulation of reactive oxygen species (ROS) and the disruption of ion homeostasis, which leads to oxidative stress and lipid peroxidation in cell membranes (Hniličková *et al.*, 2019; Dias *et al.*, 2022). The extent of damage varies among species and is influenced by the plant's ability to activate antioxidant defenses and adapt to high salinity conditions.

The higher EL and HP levels in Barhi under salinity stress indicate greater membrane damage and oxidative stress, which can disrupt cellular functions and inhibit growth. In contrast, Khalas' lower EL and HP levels suggest better membrane stability and antioxidant activity, which may contribute to its greater stress tolerance (Zhang *et al.*, 2017; Azeem *et al.*, 2023). Additionally, Khalas' lower Na⁺ accumulation under salinity stress suggests that it has more efficient ion exclusion mechanisms, preventing the toxic buildup of Na⁺ in its tissues. This is critical for maintaining cellular homeostasis and preventing the disruption of enzymatic activities and metabolic processes under salinity stress (Yaish & Kumar, 2015). Moreover, while both cultivars show increases in LP under salinity stress, Barhi exhibits higher proline accumulation compared to Khalas. Proline acts as an osmoprotectant,

helping to maintain cell turgor and protect cellular structures under stress conditions (Liang *et al.*, 2013; Singh *et al.*, 2015). However, the higher proline accumulation in Barhi may indicate that it is under greater stress compared to Khalas, which may rely on alternative stress tolerance mechanisms. In this study, Khalas exhibited lower proline accumulation alongside superior morphological and physiological performance, indicating reliance on efficient primary tolerance mechanisms—such as ion exclusion and oxidative stress mitigation—rather than osmolyte-dependent adjustment. Consequently, Barhi's elevated proline levels likely signify a compensatory response to severe cellular stress, resulting in impaired functional traits (Shafi *et al.*, 2019; Hosseinifard *et al.*, 2022).

Conclusion

This study comprehensively evaluated the effects of salinity stress on two date palm cultivars, Barhi and Khalas, revealing that under non-saline conditions, Barhi exhibited superior growth parameters such as shoot elongation rate, leaf area, leaf growth rate, and root length compared to Khalas. However, as salinity levels increased, Khalas demonstrated greater tolerance, maintaining higher growth rates, photosynthetic efficiency, and water retention under moderate (5 dS m⁻¹) and severe (6 dS m⁻¹) salinity stress, while Barhi showed a more pronounced decline, indicating higher sensitivity. Physiological and biochemical analyses further supported Khalas' superior stress tolerance, as it maintained better chlorophyll content, photosynthetic rate, relative water content, and exhibited more efficient ion homeostasis and oxidative stress management, accumulating less sodium and hydrogen peroxide and balancing proline levels more effectively than Barhi. These findings highlight Khalas as the more salt-tolerant cultivar, making it a better candidate for cultivation in saline-affected regions. Future studies should explore the genetic and molecular mechanisms underlying Khalas' salinity tolerance, conduct long-term field trials to validate its resilience, and explore breeding programs to introduce salinity-tolerant traits into high-yielding but salt-sensitive cultivars. Additionally, research on the role of beneficial soil microbes in improving salinity tolerance and growth under saline conditions could provide innovative solutions for sustainable date palm cultivation.

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References

- Abd-Elgawad, H., G. Zinta, M. Hegab, R. Pandey, H. Asard and W. Abuelsoud. 2016. High salinity induces different oxidative stress and antioxidant responses in maize seedlings organs. *Front. Plant Sci.*, 7. <https://doi.org/10.3389/fpls.2016.00276>.

- Abul-Soad, A.A., N.H. Mohamed, R. Salomón-Torres and J.M. Al-Khayri. 2023. Cultivation of date palm for enhanced resilience to climate change. In: (Eds.) Abul-Soad, A.A. and J.M. Al-Khayri. *Cultivation for Climate Change Resilience, Volume 2, Temperate Fruit Trees*. CRC Press, Taylor and Francis, Boca Raton, Florida, USA. pp. 138-169.
- Adil, M., A.N. Shah, A.N. Khan, T. Younas, M.S. Mehmood, A. Mahmood, R.M.A. Asghar and M.S. Javed., 2023. Amelioration of harmful effects of soil salinity on plants through silicon application: a review. *Pak. J. Bot.*, 55(1): 9-18.
- Al-Absi, K.M. 2023. Salinity stress in date palm (*Phoenix dactylifera* L.): tolerance, mechanisms and mitigation. *Hort. Environ. Biotechnol.*, 64(5): 695-708.
- Al-Busaidi, A., B.R. Glick and M.W. Yaish. 2022. The Effect of date palm genotypes on rhizobacterial community structures under saline environments. *Biology*, 11(11): 1666. <https://doi.org/10.3390/biology11111666>
- Al-Dakheel, A., M. Hussain, A. Abdulrahman and A. Abdullah. 2022. Long term assessment of salinity impact on fruit yield in eighteen date palm varieties. *Agric. Water Manag.*, 269: 107683. <https://doi.org/10.1016/j.agwat.2022.107683>.
- Aleid, S.M., J.M. Al-Khayri and A.M. Al-Bahrany. 2015. Date palm status and perspective in Saudi Arabia. In: (Eds.): Al-Khayri, J.M., S.M. Jain and D.V. Johnson. *Date Palm Genetic Resources and Utilization, Volume 2, Asia and Europe*. Springer Dordrecht, Netherlands. pp. 49-95. <https://doi.org/10.1007/978-94-017-9707-8>
- Alhajhoj, M.R., M. Munir, B. Sudhakar, H.M. Ali-Dinar and Z. Iqbal. 2022. Common and novel metabolic pathways related ESTs were upregulated in three date palm cultivars to ameliorate drought stress. *Sci. Rep.*, 12(1): 15027.
- Ali-Dinar, H., M. Munir and M. Mohammed. 2023. Drought-tolerance screening of date palm cultivars under water stress conditions in arid regions. *Agronomy*, 13(11): 2811.
- Al-Karmadi, A. and A.I. Okoh. 2024. An overview of date (*Phoenix dactylifera*) fruits as an important global food resource. *Foods*, 13. <https://doi.org/10.3390/foods13071024>
- Alkharabsheh, H.M., M.F. Seleiman, O.A. Hewedy, M.L. Battaglia, R.S. Jalal, B.A. Alhammad, C. Schillaci, N. Ali and A. Al-Doss. 2021. Field crop responses and management strategies to mitigate soil salinity in modern agriculture: A review. *Agronomy*, 11(11): 2299.
- Al-Khateeb, S.A., A.A. Al-Khateeb, M.N. Sattar and A.S. Mohmand. 2020. Induced in vitro adaptation for salt tolerance in date palm (*Phoenix dactylifera* L.) cultivar Khalas. *Biol. Res.*, 53: 37. <https://doi.org/10.1186/s40659-020-00305-3>
- Al-Omran, A.M., L. Dhaouadi and H. Besser. 2023. Irrigation and salinity management of date palm in arid regions. In: (Eds.) Al-Khayri, J.M., S.M. Jain, D.V. Johnson and R.R. Krueger. *Date Palm*. CABI, Wallingford, UK. pp. 241-265.
- Alotaibi, B.A., M.B. Baig, M.M. Najim, A.A. Shah and Y.A. Alamri. 2023a. Water scarcity management to ensure food scarcity through sustainable water resources management in Saudi Arabia. *Sustainability*, 15(13): 10648.
- Alotaibi, K.D., H.A. Alharbi, M.W. Yaish, I. Ahmed, S.A. Alharbi, F. Alotaibi and Y. Kuzyakov. 2023b. Date palm cultivation: A review of soil and environmental conditions and future challenges. *Land Degrad. Dev.*, 34(9): 2431-2444. <https://doi.org/10.1002/ldr.4619>
- Alumushaiti, M.A. 2024. Modernizing Saudi Arabia's dates export market via leveraging technology for sustainable growth in the global economy. *Int. J. Integrated Sci. Technol.*, 2(2): 105-120. <https://doi.org/10.59890/ijist.v2i2.1428>
- Al-Wabel, M.I., A. Sallam, M. Ahmad, K. Elanazi and A.R. Usman. 2020. Extent of climate change in Saudi Arabia and its impacts on agriculture: a case study from Qassim region. In: (Eds.): Fahad, S., M. Hasanuzzaman, M. Alam, H. Ullah, M. Saeed, I.A. Khan and M. Adnan. *Environment, Climate, Plant and Vegetation Growth*. Springer, Cham. Switzerland. pp. 635-657.
- Arif, Y., P. Singh, H. Siddiqui, A. Bajguz and S. Hayat. 2020. Salinity induced physiological and biochemical changes in plants: An omic approach towards salt stress tolerance. *Plant Physiol. Biochem.*, 156: 64-77.
- Azeem, M., K. Pirjan, M. Qasim, A. Mahmood, T. Javed, H. Muhammad, S. Yang, R. Dong, B. Ali and M. Rahimi. 2023. Salinity stress improves antioxidant potential by modulating physio-biochemical responses in *Moringa oleifera* Lam. *Sci. Rep.*, 13(1): 2895.
- Balasubramaniam, T., G. Shen, N. Esmaceli and H. Zhang. 2023. Plants' response mechanisms to salinity stress. *Plants*, 12(12): 2253. <https://doi.org/10.3390/plants12122253>.
- Bates, L.S., R.P. Waldren and I.D. Teare. 1973. Rapid determination of free proline for water-stress studies. *Plant Soil*, 39: 205-207.
- Benaceur, I., R. Meziani, J. El Fadile, J. Hoinkis, E. Canas Kurz, U. Hellriegel and F. Jaiti. 2024. Salt stress induces contrasting physiological and biochemical effects on four elite date palm cultivars (*Phoenix dactylifera* L.) from Southeast Morocco. *Plants*, 13(2): 186.
- Chen, H. and J.G. Jiang. 2010. Osmotic adjustment and plant adaptation to environmental changes related to drought and salinity. *Environ. Rev.*, 18: 309-319. <https://doi.org/10.1139/A10-014>
- Colin, L., F. Ruhnnow, J.K. Zhu, C. Zhao, Y. Zhao and S. Persson. 2023. The cell biology of primary cell walls during salt stress. *Plant Cell.*, 35: 201-217.
- Dane, J.H. and C.G. Topp. 2018. Methods of soil analysis, Part 4: Physical methods. John Wiley and Sons Inc., New Jersey, USA.
- Devkota, K.P., M. Devkota, M. Rezaei and R. Oosterbaan. 2022. Managing salinity for sustainable agricultural production in salt-affected soils of irrigated drylands. *Agric. Sys.*, 198: 103390.
- Dias, M., C. Santos, M. Araújo, P. Barros, M. Oliveira and J. De Oliveira. 2022. *Quercus suber* roots activate antioxidant and membrane protective processes in response to high salinity. *Plants*, 11. <https://doi.org/10.3390/plants11040557>.
- Dindarlou, A., A.A. Ghaemi, A.S. Nobandegani, M. Bahrami and M. Dastourani. 2019. Interaction of water salinity and different irrigation levels on physiological growth of olive (*Olea europaea* L.). *J. Agric. Sci. Technol.*, 21(6): 1623-1637.
- Dimeny, J.R. 2019. Developmental responses to water and salinity in root systems. *Annu. Rev. Cell Dev. Biol.*, 35(1): 239-257.
- Du, B., B.L. Franzisky, W. Muhammad, S. Alfarraj, C.M. Geilfus and H. Rennenberg. 2025. How to cope with stress in the Desert-the date Palm Approach. *Plant Cell Environ.*, 48(1): 768-780.
- El Rabey, H.A. 2017. Proteome of abiotic stress tolerance in date palm. In: (Eds.): Al-Khayri, J.M., S.M. Jain and D.V. Johnson. *Date Palm Biotechnology Protocols Volume II: Germplasm Conservation and Molecular Breeding*. Humana New York, USA. pp. 355-363. <https://doi.org/10.1007/978-1-4939-7159-6>
- Fiaz, S., M.A. Noor and F.O. Aldosri. 2018. Achieving food security in the Kingdom of Saudi Arabia through innovation: Potential role of agricultural extension. *J. Saudi Soc. Agric. Sci.*, 17(4): 365-375.
- Garcia, C., S. Dattamudi, S. Chanda and K. Jayachandran. 2019. Effect of salinity stress and microbial inoculations on glomalin production and plant growth parameters of snap bean (*Phaseolus vulgaris*). *Agronomy*, 9(9): 545. <https://doi.org/10.3390/agronomy9090545>.

- Guo, Q., L. Liu and B. Barkla. 2019. Membrane lipid remodeling in response to salinity. *Int. J. Mol. Sci.*, 20. <https://doi.org/10.3390/ijms20174264>.
- Hatfield, J.L. and C. Dold. 2019. Water-use efficiency: advances and challenges in a changing climate. *Front. Plant Sci.*, 10: 103. <https://doi.org/10.3389/fpls.2019.00103>
- Hazzouri, K.M., J.M. Flowers, D. Nelson, A. Lemansour, K. Masmoudi and K.M. Amiri. 2020. Prospects for the study and improvement of abiotic stress tolerance in date palms in the post-genomics era. *Front. Plant Sci.*, 11: 293.
- Hnilíčková, H., F. Hnilíček, M. Orsák and V. Hejnák. 2019. Effect of salt stress on growth, electrolyte leakage, Na⁺ and K⁺ content in selected plant species. *Plant Soil Environ.*, 65(2): 90-96. Doi. 10.17221/620/2018-PSE
- Hopmans, J.W., A.S. Qureshi, I. Kisekka, R. Munns, S.R. Grattan, P. Rengasamy, A. Ben-Gal, S. Assouline, M. Javaux, P.S. Minhas and P.A.C. Raats. 2021. Critical knowledge gaps and research priorities in global soil salinity. *Advances in Agronomy*. Elsevier Inc., Netherlands. 169: 1-191. <https://doi.org/10.1016/bs.agron.2021.03.001>
- Hosseinfard, M., S. Stefaniak, M.G. Javid, E. Soltani, L. Wojtyla and M. Garnczarska. 2022. Contribution of exogenous proline to abiotic stresses tolerance in plants: A review. *Int. J. Mol. Sci.*, 23: 5186. <https://doi.org/10.3390/ijms23095186>
- Hussain, M.I., S. Danish, S.A. Naqvi, M.J. Jaskani, M.A. Asghar, I.A. Khan, M. Munir and A. Muscolo. 2024. Physiological, biochemical, and comparative genome analysis of salt and drought stress impact on date palm (*Phoenix dactylifera* L.): tolerance mechanism and management. *Plant Growth Regul.*, 104: 1261-1283. <https://doi.org/10.1007/s10725-024-01225-y>.
- Imran, M., I. Ahmad, A. Ali, S. Basharat, M. Hameed, M.S.A. Ahmad and A. Muneeb. 2024. Modifications in anatomical traits of tall flat sedge *Cyperus exaltatus* retz. colonizing differently salt-affected wetlands. *Pak. J. Bot.*, 56(6): 2089-2096.
- Iqbal, Z. and M. Munir. 2024. Multifaceted natural drought response mechanisms in three elite date palm cultivars uncovered by expressed sequence tags analysis. *Sci. Rep.*, 14(1): 23186.
- Ji, X., J. Tang and J. Zhang. 2022. Effects of salt stress on the morphology, growth and physiological parameters of *Juglans microcarpa* L. seedlings. *Plants*, 11(18): 2381.
- Khakwani, A.A., M. D. Dennett and M. Munir. 2011. Drought tolerance screening of wheat varieties by inducing water stress conditions. *Songklanakarin J. Sci. Technol.*, 33(2): 135-142.
- Liang, X., L. Zhang, S.K. Natarajan and D.F. Becker. 2013. Proline mechanisms of stress survival. *Antioxid. Redox Signal.*, 19(9): 998-1011.
- Liao, Q., S. Gu, S. Kang, T. Du, L. Tong, J.D. Wood and R. Ding. 2022. Mild water and salt stress improve water use efficiency by decreasing stomatal conductance via osmotic adjustment in field maize. *Sci. Total Environ.*, 805: 150364. <https://doi.org/10.1016/j.scitotenv.2021.150364>
- Majeed, A. and Z. Muhammad. 2019. Salinity: A major agricultural problem-Causes, impacts on crop productivity and management strategies. In: (Eds.): Hasanuzzaman, M., K. Hakeem, K. Nahar and H. Alharby. *Plant Abiotic Stress Tolerance: Agronomic, Molecular and Biotechnological Approaches*. Springer, Cham, Switzerland. pp. 83-99. https://doi.org/10.1007/978-3-030-06118-0_3
- Medlyn, B.E., M.G. De Kauwe, Y.-S. Lin, J. Knauer, R.A. Duursma, C.A. Williams, A. Arneth, R. Clement, P. Isaac, J.-M. Limousin, M.-L. Linderson, P. Meir, N. Martin-StPaul L. and Wingate. 2017. How do leaf and ecosystem measures of water-use efficiency compare? *New Phytol.*, 216: 758-770. <https://doi.org/10.1111/nph.14626>
- Medrano, H., M. Tomás, S. Martorell, J. Flexas, E. Hernández, J. Rosselló, A. Pou, J.M. Escalona and J. Bota. 2015. From leaf to whole-plant water use efficiency (WUE) in complex canopies: Limitations of leaf WUE as a selection target. *Crop J.*, 3(3): 220-228.
- Meir, M., M. Zaccai, E. Raveh, J. Ben-Asher and N. Tel-Zur. 2014. Performance of *Ziziphus jujuba* trees correlates with tissue mineral content under salinity conditions. *Agric. Water Manag.*, 142: 47-55. <https://doi.org/10.1016/J.AGWAT.2014.05.002>.
- Munir, M., M.R. Alhajhoj, M.E. Mohammed, H.S. Ghazzawy, M.M. Elgarawany, M.S. El-Habbab, F.I. Zeineldin and A.M. Al-Bahigan. 2020. Effects of date palm biochar on growth, yield and photosynthetic capacity of cucumber (*Cucumis sativus* L.) under glasshouse conditions. *Pak. J. Life Soc. Sci.*, 18(1): 7-16.
- Munns, R. and M. Tester. 2008. Mechanisms of salinity tolerance. *Annu. Rev. Plant Biol.*, 59(1): 651-681.
- Pan, T., M. Liu, V.D. Kreslavski, S.K. Zharmukhamedov, C. Nie, M. Yu, V.V. Kuznetsov, S.I. Allakhverdiev, and S. Shabala. 2021. Non-stomatal limitation of photosynthesis by soil salinity. *Crit. Rev. Environ. Sci. Technol.*, 51(8): 791-825.
- Pitman, M.G. and A. Läuchli. 2002. Global impact of salinity and agricultural ecosystems. In: (Eds.): Läuchli, A. and U. Lüttge. *Salinity: Environment-Plants-Molecules*. Springer, Dordrecht, Netherlands. pp. 3-20. https://doi.org/10.1007/0-306-48155-3_1
- Rewald, B., O. Shelef, J.E. Ephrath and S. Rachmilevitch. 2013. Adaptive plasticity of salt-stressed root systems. In: (Eds.): Ahmad, P., M.M. Azooz and M.N.V. Prasad. *Ecophysiology and Responses of Plants under Salt Stress*. Springer New York, USA. pp. 169-201. <https://doi.org/10.1007/978-1-4614-4747-4>
- Riseh, R., M. Ebrahimi-Zarandi, E. Tamanadar, M. Pour and V. Thakur. 2021. Salinity stress: Toward sustainable plant strategies and using plant growth-promoting rhizobacteria encapsulation for reducing it. *Sustainability*, 13(22): 12758. <https://doi.org/10.3390/su132212758>.
- Sairam, P.K. and G.C. Srivastava. 2002. Changes in antioxidant activity in sub-cellular fractions of tolerant and susceptible wheat genotypes in response to long-term salt stress. *Plant Sci.*, 162: 897-904
- Sajid, Z.A. 2023. Effect of salinity on growth and physiology of *Thellungiella halophila* L. ecotypes. *Pak. J. Bot.*, 55(1): 1-8.
- Samarah, N.H. 2005. Effects of drought stress on growth and yield of barley. *Agron. Sustain. Dev.*, 25(1): 145-149.
- Shafi, A., I. Zahoor and U. Mushtaq. 2019. Proline accumulation and oxidative stress: Diverse roles and mechanism of tolerance and adaptation under salinity stress. In: (Ed.): Akhtar, M. *Salt Stress, Microbes, and Plant Interactions: Mechanisms and Molecular Approaches*. Volume 2. Springer, Singapore. pp. 269-300. https://doi.org/10.1007/978-981-13-8805-7_13
- Shelden, M.C. and R. Munns. 2023. Crop root system plasticity for improved yields in saline soils. *Front. Plant Sci.*, 14: 1120583.
- Shetty, P., M.M. Gitau and G. Maróti. 2019. Salinity stress responses and adaptation mechanisms in eukaryotic green microalgae. *Cells*, 8(12): 1657. <https://doi.org/10.3390/cells8121657>
- Singh, M., J. Kumar, S. Singh, V.P. Singh and S.M. Prasad. 2015. Roles of osmoprotectants in improving salinity and drought tolerance in plants: a review. *Rev. Environ. Sci. Biotechnol.*, 14: 407-426.

- Tanou, G., P. Filippou, M. Belghazi, D. Job, G. Diamantidis, V. Fotopoulos and A. Molassiotis. 2012. Oxidative and nitrosative-based signaling and associated post-translational modifications orchestrate the acclimation of citrus plants to salinity stress. *Plant J. Cell Mol. Biol.*, 72(4): 585-599. <https://doi.org/10.1111/j.1365-313X.2012.05100.x>.
- Velikova, V., I. Yordanov and A. Edreva. 2000. Oxidative stress and some antioxidant systems in acid rain-treated bean plants: Protective role of exogenous polyamines. *Plant Sci.*, 151: 59-66.
- Xiao, F. and H. Zhou. 2022. Plant salt response: Perception, signaling, and tolerance. *Front. Plant Sci.*, 13: 1053699.
- Yaish, M.W. and PP. Kumar. 2015. Salt tolerance research in date palm tree (*Phoenix dactylifera* L.), past, present, and future perspectives. *Front. Plant Sci.*, 6: 348. doi: 10.3389/fpls.2015.00348
- Yi, K., J.T. Maxwell, M.K. Wenzel, D.T. Roman, P.E. Sauer, R.P. Phillips and K.A. Novick. 2019. Linking variation in intrinsic water-use efficiency to isohydricity: a comparison at multiple spatiotemporal scales. *New Phytol.*, 221(1): 195-208.
- Yusuf, N., C. Kooli, H. Khoj and N.O. Bajnaid. 2025. Strategizing sustainable food security in Saudi Arabia: A policy and scenario approach to agricultural resilience. *Outlook Agric.*, 54(1): 77-90. <https://doi.org/10.1177/00307270241302091>
- Zahra, N., M.S. Al Hinai, M.B. Hafeez, A. Rehman, A. Wahid, K.H. Siddique and M. Farooq. 2022. Regulation of photosynthesis under salt stress and associated tolerance mechanisms. *Plant Physiol. Biochem.*, 178: 55-69.
- Zhang, W., Z. Xie, L. Wang, M. Li, D. Lang and X. Zhang. 2017. Silicon alleviates salt and drought stress of *Glycyrrhiza uralensis* seedling by altering antioxidant metabolism and osmotic adjustment. *J. Plant Res.*, 130: 611-624.

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