



Adaptive responses of *Moringa oleifera* to hydric and saline stress and associated changes in bioaccumulated proline

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Abstract

This study evaluated the effects of saline groundwater irrigation on the growth and physiological response of *Moringa oleifera*. Groundwater used for irrigation was analyzed for its physicochemical properties, and plant responses were assessed through growth measurements and leaf proline accumulation.

The water showed a slightly alkaline pH and an electrical conductivity of 11.5 mS cm⁻¹, indicating slight salinity. Potassium concentration was 10.4 mg L⁻¹, and the high calcium and magnesium levels reflected water hardness. The soil, however, had low CaCO₃ content and a relatively high organic matter percentage. Saline irrigation reduced plant growth but significantly increased leaf proline content compared with plants irrigated with non-saline water. *M. oleifera* tolerated salinity levels of 2 to 6 g L⁻¹ and adapted by producing a more branched root system to improve water and nutrient uptake.

These findings show that *M. oleifera* possesses notable tolerance to salinity and water stress, supporting its potential for cultivation in arid zones, sebkhas, and saline soils, and for large-scale production for medicinal uses.

1. INTRODUCTION

Soil salinity is a major constraint on agricultural productivity, and its severity is increasing due to climate change and poor land and water management (Ding et al., 2021; Atteya et al., 2021). The expansion of salt-affected soils contributed to land degradation, reduced crop yields, and economic losses (Singh, 2021). Salinity is particularly damaging under deficit irrigation, where osmotic and ionic stresses become more pronounced (Elgallal et al., 2016; Nagaz et al., 2012). Long-term use of wastewater for irrigation can accelerate salinization, highlighting the need for adequate management practices such as leaching and drainage (Elgallal et al., 2016; Yang et al., 2019). Plants exposed to abiotic stress commonly experienced osmotic, ionic, and oxidative stress, accompanied by nutrient imbalance (Ma et al., 2020). Water stress and high evaporation rates further reduced seed germination, vigor, growth, and phytochemical

composition (Fazlali et al., 2013; Lahmar et al., 2023).

Moringa oleifera is widely recognized for its nutritional and medicinal value and is increasingly promoted as a tool to combat malnutrition. It exhibits diverse biological and therapeutic activities, including antimicrobial, antioxidant, anti-inflammatory, antidiabetic, antihypertensive, antipyretic and anticancer properties (Zayas-Viera et al., 2016; Metwally et al., 2017; Farooq and Koul, 2020; Padayachee and Baijnath, 2020).

The seeds, often considered by-products, have recently attracted attention. Studies showed that salinity does not significantly affect seed oil content, although it may alter tocopherol and fatty acid profiles (Anwar et al., 2005; Al-Shoaibi and Boutraa, 2021). Other research has demonstrated that *M. oleifera* tolerated moderate salinity through activation of physiological and biochemical defense systems, which help mitigate

ion toxicity and oxidative stress (Nouman et al., 2012; Azeem et al., 2023).

Despite these findings, information remains limited regarding the combined effects of salinity and water stress on the vegetative growth of *M. oleifera*. Hence, this study aimed to assess the effects of groundwater irrigation and particular soil composition on the growth of *M. oleifera* and on proline accumulation under varying field capacities and salinity levels.

2. MATERIALS AND METHODS

2.1. Physico-chemical analysis of irrigation water

The physicochemical analysis of the irrigation water used in the stress application (groundwater) allows for an assessment of water quality and its compatibility with the soil used. The pH value was determined using a digital pH meter, and electrical conductivity was measured with a conductivity meter (APHA, 1998). Total dissolved constituents corresponding to the total amount of particulate matter dissolved in a given volume of water was determined (Cravotta and Brady, 2015).

The determination of carbonates is carried out when the pH of the saturated extract was superior or equal to 8.3. Titrate using the flame spectrophotometer was followed to determine potassium and sodium amounts. The titration procedure with silver nitrate led to determine the chlorides amount (Boltz and Howell, 1978). The hardness of water is assessed through the complexometric titration of the combined levels of calcium and magnesium using EDTA (Tucker and Kurtz, 1961). A turbidimetric analytical assay was followed to determine the sulfate amount (Tabatabai and Bremner, 1970).

2.2. Physico-chemical analysis of agricultural soil

pH value was determined. The electrical conductivity (EC) of the soil, indicating the soluble salt content, was assessed by employing an EC meter with a 200g of saturated soil paste (AFNOR, 1987). The total content of calcium carbonate was assessed using the volumetric

method where the percentage of CaCO_3 involved the volume of CO_2 released during calibration. The assessment of carbon levels was conducted using a calorimetric method at 600 nm on the soil specimens (Walkey-Black, 1934). The determination of total potassium known as exchangeable potassium was carried out and obtained solutions were subjected to a flame spectrophotometer. Assimilable P_2O_5 were quantified at 660 nm (Celik et al., 2005).

2.3. Study of the effect of saline and water stress on the vegetative behavior of *Moringa*

2.3.1. Cultivation of *Moringa oleifera* seeds

60 seeds were soaked in a bowl of water for at least 24 hours to accelerate germination, and the outer seed coat was discarded. A mixture of three parts potting soil and one part sand was prepared. Forty seeds are sown at a depth of 7 mm. The pots were watered and placed in a warm location (in the glazed greenhouse at Bio-resources Laboratory of Integrative Biology and Valorisation, Higher Institute of Biotechnology of Monastir, Tunisia) to expedite germination. The soil was kept consistently moist with frequent watering but not waterlogged. Germination occurred 4 days after sowing. Due to a lack of ventilation in the greenhouse and rising temperatures (50°C), the pots were moved outside the greenhouse. Watering continues until the plants develop their first two pairs of leaves. Thus, two types of stress were applied when the stem length exceeded 10 cm. These seedlings underwent normal irrigation and stress irrigation. This was carried out over a period of 3 months (April, May, and June) with irrigation conducted following Table 1.

For salt stress, groundwater, well water, with a concentration of 8 g/L was used. From this concentration, dilutions of the three other irrigation concentrations (2 g/L, 4 g/L, and 6 g/L) were prepared. Whereas, for water stress, tap water was used.

2.3.2. Germination rate in %

The germination rate indicated how many seeds of a plant species, variety, or specific seed lot were likely to germinate over a given period

Table 1. Irrigation conditions

Treatment	Water stress			Salt stress		
	FC control	1/2 FC	1/4 FC	2 g/L	4 g/L	6 g/L
Volume	237 ml	118.5 ml	59.25 ml	250 ml	250 ml	250 ml

FC: field capacity, was the maximum water retention capacity of the soil. It more precisely corresponded to the amount of water held after 48 hours.

(germination capacity). It measured the progression of germination time and was typically expressed as a percentage. The germination rate in percentage is calculated as (Number of germinated seeds/Number of seeds tested) multiplied per 100.

2.3.3. Proline assay

For each type of stress, 6 plants were studied. Samples were collected, preserved, dried, and ground. The extraction process required grinding and homogenizing 0.5 g of stem and root in 10 ml of 3% sulfosalicylic acid. The extract undergoes centrifugation at a speed of 10,000 rpm/min for 15 min. For proline quantification, 2 ml of the supernatant was mixed with 2 ml of ninhydrin reagent and 2 ml of glacial acetic acid. Allowed to react for 1 hour at 100°C, the mixture was then cooled in ice. Extracted involved an ad of 4 ml of toluene and stirring for 15 to 20 s. Leaved at room temperature for 30 min, the toluenic phase was extracted from the mixture. The absorbance was measured at 520 nm against toluene (Bates et al., 1973).

2.4. Statistical analysis

The results of different analyses were presented as mean ± standard error (SD). Statistical studies were conducted using SPSS 18.0 (Statistical Package for Social Sciences) software. Comparisons between the results of different stresses were performed by applying the one-way analysis of variance (ANOVA) followed by the LSD test (Least Significant Difference). Differences are considered statistically significant when $p < 0.05$.

3. Results

3.1. Physicochemical analysis of irrigation water

The pH value of irrigation water was 7.54. In addition, the electrical conductivity value was around 11.5 mS cm⁻¹. Consequently, the salinity was equal to 8.05 g L⁻¹. The irrigation source was considered highly saline. The used irrigation water in this study has no carbonate content, whereas the bicarbonates measured 217.7 mg L⁻¹ (Table 2).

Table 2. Amounts of carbonates and bicarbonates in irrigation water

Mineral element	Concentration (mg L ⁻¹)	Concentration (meq L ⁻¹)
CO ₃ ²⁻	0	0
HCO ₃ ⁻	217,7	3,57

The concentration of total dissolved constituents was 9.01 g L⁻¹. The levels of potassium and sodium were defined respectively, 10.4 and 200 mg L⁻¹. Chlorides analysis revealed that the irrigation water presented a high level with an amount of 426 mg L⁻¹. A high level of calcium and magnesium was revealed with 180 mg L⁻¹. The water used for irrigation has a very high sulfate content equal to 289.47 mg L⁻¹.

3.2. Physico-chemical analysis of agricultural soil

The analyzed sample has a slightly acidic pH with a value of 6.21. In case of the selected soil to growing *M. oleifera* seeds, the EC was about 4.74 mS cm⁻¹. By deduction, the salinity is equal to 3.31 g L⁻¹. The result of the total limestone content analysis showed that the percentage of CaCO₃ was low, around 0.9%.

The result of the organic carbon content analysis showed that the percentage of carbon was approximately 3.5%. The percentage of organic matter was 6.03% which signified that the soil was rich in organic matter. However, the soil presented quantities of 503 and 57 mg/kg for potassium and phosphorus, respectively.

3.3. Effect of saline and water stress on the vegetative behavior of *M. oleifera*

In the absence of ventilation, the temperature rose to 55°C, leading to a rapid yellowing and wilting of the seedlings. To avoid this temperature stress, the pots were transferred to the open garden. A few days later, symptoms of etiolation were observed in the seedlings, with elongation and weakening of the stems, eventually leading to death. For the first cultivation, the germination rate was 92.8%.

In the second cultivation, 42 seedlings were obtained with a germination rate of 83.3%. The proline contents of stressed plants were presented in Fig. 1. *M. oleifera* plants irrigated with saline water showed a significantly higher accumulation of proline compared to the control plants. The maximum proline levels obtained from media composed of 6 g/L of well water salt were approximately 6 to 7 times higher than those in the control plants. Indeed, the statistical analysis results of proline content demonstrated a significant difference ($P < 0.05$) among the various cases.

Furthermore, the proline levels obtained under water stress were almost the same as those stressed by an increase in salt concentration. A substantial accumulation of proline, around 0.15

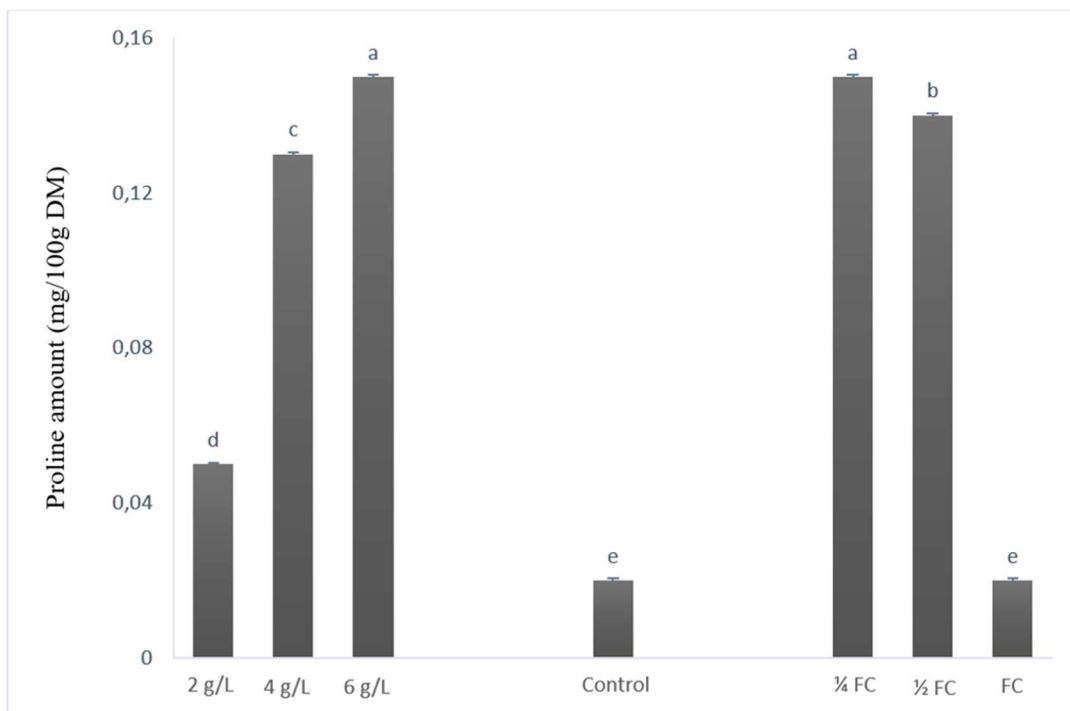


Fig. 1. Proline contents in *M. oleifera*, control, and stressed plants (mg/100g DM). Values not followed by the same letters (a, b, c, d, and e) on the bars in the same histogram are significantly different at $p < 0.05$.

mg/100g DM, was observed in plants irrigated with a water volume of $\frac{1}{4}$ FC corresponding to 59.25 ml. Data analysis indicated that the effect of salinity on proline accumulation was significant, since this amino acid expressed higher levels compared to the controls. Similarly, water deficiency caused nearly the same effects on plant growth from a physiological perspective, as proline accumulation evolved almost proportionally with the intensity of water stress.

4. Discussion

Plants are sensitive to inappropriate pH ranges, which can cause abnormal growth variations (Ayers and Westcot, 1985). The findings showed a slightly alkaline pH. In fact, the pH of irrigation water should ideally be between 6.0 and 8.5 (FAO, 1985). At these levels, the solubility of most micronutrients was optimal. The water posed risks during irrigation as the bicarbonate content was classified as hard ($3.57 \text{ meq L}^{-1} > 2.5 \text{ meq L}^{-1}$, according to the FAO (1985) irrigation water quality guidelines). Excessive salt content in irrigation water is a major concern, as high salt concentrations in water or soil can adversely affect crop yield, lead to soil degradation, and contaminate groundwater (Mohanavelu et al., 2021). The suitability of saline water for irrigation depended on several factors, including the salt tolerance of cultivated plants and the

characteristics of the soil (Ben Ahmed et al., 2012). Indeed, improper irrigation can result in salinization, reduced crop yield, and amplified spatial variations in soil moisture (Cheng et al., 2021). Water with total dissolved constituents below 0.45 g L^{-1} is considered suitable for irrigation for agricultural purposes (FAO, 2006). The irrigation water used for *Moringa* cultivation showed a high value, falling within the mild to moderate restriction range. The dissolved residues originated from natural mineral sources and anthropogenic inputs, including agrochemicals (Kundi, 2012).

Bicarbonates were the most abundant ions in the irrigation water and constituted the main elements in groundwater (Demelash et al., 2023). Their concentrations were below the WHO standard of 250 mg L^{-1} (Kouamé et al., 2011). Potassium levels were below WHO limits (12 mg L^{-1}), while sodium exceeded the standard (150 mg L^{-1}) (Kouamé et al., 2011). Potassium plays a key role in drought and disease resistance and root development. Sodium, at certain concentrations, is responsible on the osmotic pressure regulation of plant cells, improving water use efficiency, but excess sodium affects soil permeability and infiltration (Gong, 2021). Accumulation of sodium in the soil can deplete soil organic carbon and hinder the nitrogen cycle

(Rowley et al., 2018). Based on the sodicity or sodium absorption ratio (SAR), the water was suitable for irrigation. However, chloride levels were high, exceeding WHO standards of 250 mg L⁻¹ (Kouamé et al., 2011), and may induce toxicity in sensitive crops. High chloride concentrations can cause leaf burning and tissue desiccation, and affect soil water retention and soil organisms, reducing overall productivity (White and Broadley, 2001; Rietz and Haynes, 2003). Moreover, chloride and sodium ions can influence the release and transport of heavy metals, such as lead and palladium, into the soil (Pahlavan et al., 2023).

The hydrometric degree, reflecting water mineralization, is proportional to the concentrations of calcium and magnesium, occasionally augmented by iron, aluminum, and manganese (Benaricha et al., 2017). The analyzed water had a high level of calcium and magnesium (180 mg/L), exceeding the WHO standard of 150 mg L⁻¹ (Kouamé et al., 2011). Water hardness, arising from calcium and magnesium, was therefore high. Calcium contributed to soil structure improvement and regulated soil acidity (Brock et al., 2021). Sulfur, an essential element for plant growth, is involved in amino acids, vitamins metabolism, and stress tolerance mechanisms (Narayan et al., 2022; Li et al., 2020). Predominant groundwater ions, including potassium, sodium, calcium, and magnesium, were related to the geochemical processes and water-rock interactions, and their concentrations vary depending on geographical and anthropogenic activities (Huang and Ma, 2019).

The pH of agricultural soil affects its physical, chemical, and biological behavior, including organic matter mineralization (Rasool et al., 2022). Most cultivated plants grow optimally near neutrality (6.5–7.5). Increased soil acidity can reduce plant vitality, impair root growth, and increase susceptibility to disease (Agegnehu et al., 2021). Soil electrical conductivity reflected total ion concentrations, and high EC indicated saline conditions (Şener et al., 2021). The presence of limestone in the soil can challenge plant development, as only limestone-tolerant species grow normally; otherwise, growth difficulties and physiological disorders may occur (Lahmar et al., 2023). High organic matter enhanced soil stability, water absorption, and prevented erosion (Maietta et al., 2019). The soil analyzed was rich in potassium and phosphorus, linked to organic matter content and microbial

degradation (Khan et al., 2013). Insufficient nutrients negatively affect growth, morphology, and physiology of plants (Al-Humaid, 2005). Differences in soil physicochemical and biological properties were closely linked to variations in plant growth, development, and nutrient composition, impacting the plant's bioactive components (Lahmar et al., 2023).

The biochemical response of *M. oleifera* to salinity and water stress, evaluated through proline accumulation, showed variability in both concentration and stress intensity. The species tolerated salinity of 2 g L⁻¹, adapting primarily through root branching to improve nutrient and water uptake. These results align with previous investigations (Wassif et al., 2012). Variations in proline accumulation reflected the species' ability to withstand threshold salt concentrations. Proline served as a stress indicator, functioning as a compatible osmolyte to maintain cell turgor, stabilize membranes, and act as a reserve of carbon and nitrogen (Tandra et al., 2022; Hayat et al., 2012; Hosseinifard et al., 2022; Denden et al., 2005; Keller et al., 1993). Additionally, it regulated redox potential by diminishing oxygenase and carboxylase activities (Misra and Saxena, 2009; Kaur and Asthir, 2015). Proline accumulation is thus a key strategy for *M. oleifera* to resist water and salt stress.

This study highlighted the potential of using groundwater for irrigating *M. oleifera*. The water exhibited slight salinity, while the soil was rich in organic matter. Foliar proline accumulation under saline or water stress revealed a response similar to that of halophytes. According to Braun-Blanquet classification of halophytes into oligo-, meso-, and euhalophytes based on salinity tolerance (Braun-Blanquet, 1931), *M. oleifera* may align with the oligohalophyte group. Comparable responses are observed in other moderately tolerant halophytes. In the Mediterranean *Atriplex halimus*, proline increased significantly under salt stress, aiding osmotic adjustment and stress resistance (Ben Hassine and Ghanem, 2008). Likewise, species of the genus *Suaeda*, such as *S. monoica*, accumulated proline under salinity, particularly when combined with drought, highlighting its role as an osmoprotectant (Yadav et al., 2021). These findings indicated that *M. oleifera*, under 2–6 g L⁻¹ NaCl, employed mechanisms typical of moderately tolerant halophytes, using proline to maintain cellular homeostasis under salinity.

Comparison with previous studies on *M. oleifera* confirmed a consistent pattern of proline

accumulation under salt stress. Plants exposed to 50–100 mM NaCl showed marked increases in proline and soluble sugars, reflecting effective osmotic adjustment (Azeem et al., 2023). Elevated free proline levels were also reported in salt-stressed moringa trees, reinforcing its role as a primary osmo-protectant (Bayomy et al., 2025). Overall, *M. oleifera* demonstrates the capacity to synthesize and accumulate proline in response to saline conditions, highlighting its adaptive potential and suitability for cultivation in marginal or saline environments.

5. Conclusions

In conclusion, the study elucidated the use of groundwater for irrigating *Moringa oleifera* plants. The water displayed a slightly salinity. Noteworthy organic matter percentage characterized the studied soil. The biochemical response evaluated through the process of foliar proline accumulation in the species *M. oleifera* under saline or water stress has revealed a behavior similar to halophytes. These plants demonstrate their ability to synthesize and accumulate proline. The accumulation of this organic compound is a phenomenon primarily associated with saline conditions. Given its robust adaptive features, *M. oleifera* emerges as a promising candidate for cultivation.

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