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Original Article

Physiological Adaptation of Three Halophytes from the Same Ecological Habitat and Analysis of their Supporting Soil

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ABSTRACT

Objectives: This study was conducted to investigate the physiological adaptations and metabolic responses of three halophytes: *Pulicaria undulata*, *Tamarix nilotica*, and *Lycium shawii*—during their flowering stage under abiotic stress conditions in Sabkhat Al-Awshaziyah. The study aimed to assess the physical and chemical characteristics of the rhizosphere soils associated with these species.

Material and Methods: Rhizosphere soil samples were collected from around each species and analyzed for their physical properties, including soil texture and hydraulic conductivity, as well as chemical properties such as cation exchange capacity (CEC) and organic matter (OM) content. To understand plant responses to salinity stress, several physiological and biochemical parameters were measured, including leaf area, total carbohydrate content, photosynthetic pigments (chlorophyll and carotene), and antioxidant enzyme activities (peroxidase and polyphenol oxidase).

Results: The rhizosphere soils were predominantly sandy. Soils associated with *L. shawii* and *P. undulata* showed a medium-coarse texture, while those of *T. nilotica* were fine sandy. Hydraulic conductivity values were relatively high, ranging from 23.33 to 27 cm h^{-1}. Overall, soil fertility was low, as reflected by CEC and OM values. The highest CEC was recorded in *T. nilotica* soil, reaching 12.3 Meq/100 g in the subsurface and 11.27 Meq/100 g at the surface, whereas *L. shawii* exhibited the lowest values at both depths. Organic matter content followed a similar trend, with *T. nilotica* showing the highest percentages (0.83% at the surface and 0.74% in the subsurface). In contrast, *P. undulata* and *L. shawii* displayed comparable but lower OM values.

Regarding physiological traits, *T. nilotica* had the smallest leaf area (0.66 cm^2/plant) but accumulated the highest carbohydrate content (31.5%). *L. shawii* recorded the lowest carbohydrate level (16.8%). Pigment analysis revealed that *P. undulata* contained the highest levels of chlorophyll and carotene. In terms of antioxidant activity, peroxidase activity was highest in *L. shawii* (477.33 u/g fresh weight/h), while *P. undulata* showed the greatest *polyphenol oxidase* activity (38.94 u/g fresh weight/h).

Conclusion: The results demonstrate that the studied halophytes employ different adaptive strategies to cope with saline stress. *T. nilotica* appears to benefit from relatively better soil conditions and higher carbohydrate accumulation, *P. undulata* maintains stronger photosynthetic pigment levels, and *L. shawii* exhibits enhanced antioxidant enzyme activity. Collectively, these findings highlight the ecological significance and practical value of these species as potential candidates for the conservation and rehabilitation of saline areas.

Key words: Antioxidants Enzymes, *Lycium Shawii,* Osmolytes, *Pulicaria Undulata,* Sabkha, Salinity, *Tamarix Nilotica*

INTRODUCTION

About 70% of the world's land area is threatened by soil salinity, which disrupts agricultural lands and causes plant production imbalances.[1] Locally, 40% of Saudi agricultural land suffers from salinity due to improper irrigation methods, according to the Saudi Ministry of Environment, Water and Agriculture (2017).[2] Moreover, Saudi Arabia is characterized by high salinity, shallow waters, and elevated temperatures, as well as severe desert environments without lakes or rivers.[3,4] Therefore, salt stress is a significant environmental factor that limits plant growth, crop production, and distribution.[5] Sabkhas are salt-affected areas widely distributed throughout the Kingdom of Saudi Arabia. They are known for their adaptability to severe environmental conditions, due to their elevated saline content and drought-tolerant ecosystems, in which particular halophytic plants have adapted to grow.[6] Generally, the Qassim Region of Saudi Arabia has a high-salinity ecosystem, which affects plant growth and is a major challenge behind the slow agricultural development in the area.[7] The habitat-related effects and environmental factors associated with desert climates, high salinity, and water and nutrient shortages have underscored the importance of halophytic plants in the fields of alternative medicine and drug discovery.[8] Sabkhat Al-Awshaziyah is located in the

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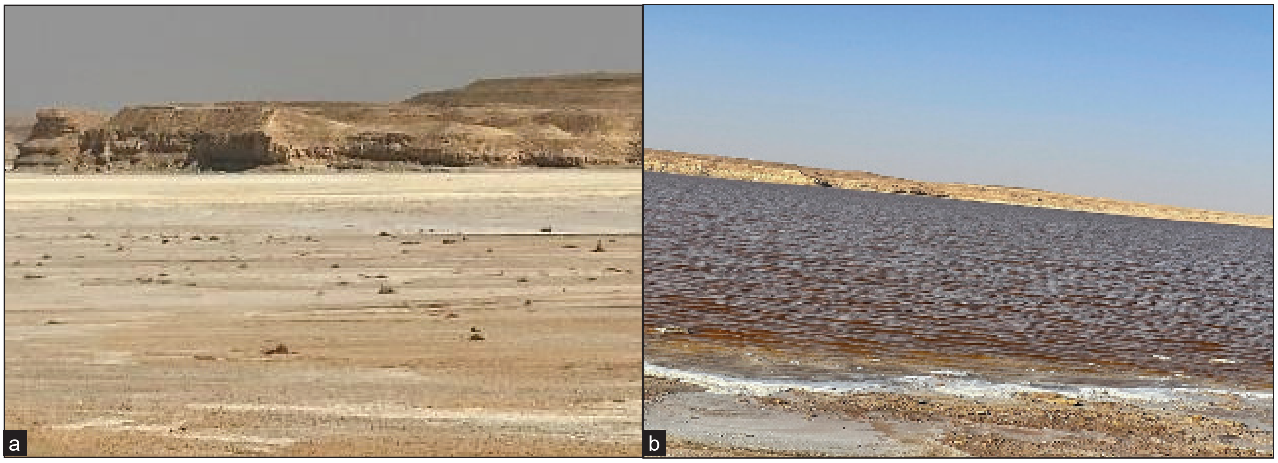

Figure 1: Pictures of Sabkhat Al-Awshaziyah location in different seasons. (a) Sabkhat Al-Awshaziyah in the summer after water dryness and accumulation of salt residues, (b) same location in the winter where salt precipitations are shown on the edges (N 26° 03' 53.63"; E 44° 09' 17.42").

Qassim region, 15 km east of the city of Unaiza, with a total area of approximately 18 square km. It has a geological impact in Saudi Arabia due to its extreme salinity [Figure 1].[9]

One potential solution to address the elevated salinity problem is to cultivate halophytic crop species, which are resistant to severe salinity stress.[10] Halophytes are plants that can survive in media containing up to 200 mM or more NaCl, and they are part of various angiosperm families with polyphyletic origins of salt tolerance.[11] Severe environmental conditions cause plants to maintain higher levels of defensive compounds, which are produced as part of their survival mechanisms against bacterial infection, excessive oxidative stress, and animal grazing.[12] For instance, the relatively higher levels of secondary metabolites, such as flavonoids, saponins, alkaloids, and phenolics, make these plants more intriguing for biological and chemical evaluations.[13] Additionally, these compounds also contribute to significant health-promoting and nutritional benefits against reactive oxygen species (ROS) by producing phenolic and flavonoid compounds to neutralize their harmful effects as part of their antioxidant defense systems. Locally, halophytes are also used as livestock feed and for treating medical conditions among ailing populations.[14,15]

Moreover, halophytes can grow under toxic conditions in metal-polluted soil due to their antioxidant systems, which also contribute to their salt tolerance and to their survival even in the presence of other non-halophytes in their surrounding area. These factors make a very promising impact of halophytes on both humans and the environment. In addition, they provide us with a new direction in the utilization and development of saline-alkali soils that assures sustainability.[16] Adaptation to saline soils results from modifications in biophysical, physiological, morphological, and biochemical traits of plants.[17] For instance, activating enzymatic antioxidants such as superoxide dismutase, peroxidase, and phenol oxidase, as well as non-enzymatic antioxidants such as flavonoids and phenolic compounds, modulating carotenoid levels, promoting chlorophyll (Chl) synthesis to sustain the photosynthetic system, regulating ROS production, and producing osmoregulatory and compatible solutes like proline.[18] Therefore, the growth of halophytic plants would offer a sustainable strategy to restore soil salinity and to exploit limited water resources, thereby allowing agriculture to move into previously barren areas of salt marshes.[16]

Pulicaria undulata

Pulicaria undulata (*P. undulata*), with the local name "Gethgath," is a high-salt-tolerant plant genus belonging to the Asteraceae family, which includes more than 100 herbaceous plants. These species are ubiquitous in high-salinity soils and dry areas of the Qassim region in Saudi Arabia. Furthermore, they are characterized by their adaptation to survive in harsh conditions through biochemical and morphological mechanisms.[19]

P. undulata is a perennial bush native to Saudi Arabia, and its average height is 40-50 cm and extends almost to a meter with several branches emanating from the plant's base. The flowers appear in the spring (February-April) in the form of 8 mm yellow knots and have an aromatic smell [Figure 2]. Interestingly, *P. undulata* is highly useful for rehabilitating natural vegetation. It can be used with various plant seed mixtures to restore vegetation in a particular area or strengthen the ecosystem.[20]

Tamarix nilotica

Tamarix nilotica (*T. nilotica*), with the local names "Athel" and "Tarfa," is a perennial small bush belonging to the

Figure 2: Pictures of *P. undulata* in different seasons. (a) *P. undulata* in the flowering phase during the spring season. (b) Demonstration of dryness on most *P. undulata* flowers during the summer season (N 26° 04' 9.94"; E 44° 09' 57.83").

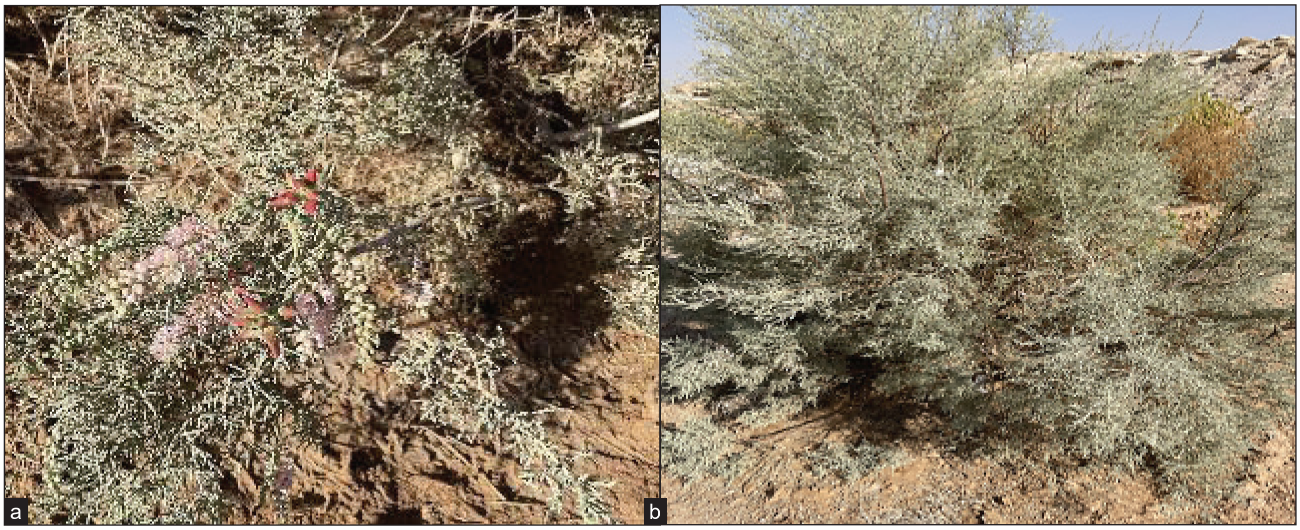

Figure 3: Pictures of *T. nilotica* in different seasons. (a) *T. nilotica* branch at the flowering phase in the spring season. (b) *T. nilotica* in summer showing green-greyish color (N 26° 04' 3.78"; E 44° 09' 48.98").

Tamaricaceae family and is distributed in the Arabian Peninsula and North Africa [Figure 3]. It is characterized by its slow, irregular growth, reaching heights of up to 8 m, and by having multiple stems. Moreover, the flowering phase occurs in March to May, and the plant has no requirements for soil or irrigation due to its high tolerance to high salinity, as well as its adaptation to drought and wind. In addition, it is used to stabilize banks and slopes and to strengthen the ecosystem through its dense, branched roots. Notably, the plant has salt glands, which contribute to its high salinity tolerance.[20]

Lycium shawii

Lycium shawii (L. shawii), with the local name "Awsaj," is a perennial bush belonging to the Solanaceae family, spread across the Arabian Peninsula, Egypt, Sudan, and Palestine [Figure 4]. Its average height ranges from 1-2 m. Furthermore, the flowering phase occurs from November-June. Notably, the wood of this plant can be used as fuel due to its low smoke output.[21]

L. shawii is adapted to desert conditions and can withstand drought, high temperatures, frost, wind, and grazing. It is highly saline-tolerant and almost does not need irrigation once its seeds germinate. It is used as a predominant plant for hillside planting, slope stabilization, and environmental improvement.[20]

Therefore, the present study aims to assess the physical and chemical analyses of Sabkhat Al-Awshaziyah soil. In addition, three naturally growing halophytes from the area have been selected for physiological and chemical studies: *Pulicaria*

Figure 4: Pictures of *L. shawii* in different seasons. (a) *L. shawii* flowers during November-June period. (b) falling *L. shawii* leaves in the summer (N 26° 04' 6.17"; E 44° 09' 57.67").

undulata, *Tamarix nilotica*, and *Lycium shawii*. These halophytes and their supporting soils might help in understanding the underlying mechanisms of their powerful ability to withstand harsh conditions and contribute to ecosystem sustainability, in addition to their economic and biological value.

MATERIAL & METHODS

The current study was conducted on three naturally occurring halophytes (*P. undulata, T. nilotica, and L. shawii*) from Sabkhat Al-Awshaziyah in the Qassim Region, Saudi Arabia (N 26° 03' 53", E 44° 09' 17"). The samples were collected in the period from March-April, 2023. Nine homogeneous, medium-sized plants were selected to represent halophytes at the flowering stage in the selected area and labeled for the collection of plant leaves for physiological analyses. The soil samples were collected from under the same marked plants at two depths (0-15 cm and 15-30 cm), placed in sterile plastic containers, and brought to the laboratory for physical and chemical analyses.

Soil physical analysis

The disturbed samples were used to determine particle size distribution, bulk density (Db), particle density (Dp), and total porosity (P%) according to Burt's (2014) method.[22] Additionally, hydraulic conductivity (HC) was estimated according to Page (1982).[23]

Particle size distribution

The particle size distribution of the soil samples was estimated using sodium hexametaphosphate as a dispersion agent by the pipette method.

Bulk density (Db)

The bulk density values were determined using undisturbed soil cores according to the following formula:

$$\mathrm{Db} = \frac{\mathbf{Ms}}{\mathbf{Vt}}$$

Where: Db = Bulk density (g cm^{-3}), Ms = Dry mass of soil in core (g), and Vt = Total volume of soil (particles plus pores) in core (cm^{3}).

Particle density (Dp)

A pycnometer determined the Dp values according to the following formula:

$$\mathrm{Dp} = \frac{\mathbf{Ms}}{\mathbf{Vs}}$$

Where: Dp = Particle density (g cm^{-3}), Ms = Dry mass of soil in core (g), and Vs = The volume of soil particle (cm^{3}).

Total porosity (P%)

The total porosity was calculated using the following formula:

$$P = 100\left(1 - \frac{Db}{Dp}\right)$$

Where: P = Total porosity, Db = Bulk density (g cm^{-3}), and Dp = Particle density (g cm^{-3}).

HC

The HC was estimated by the constant-head method, in which 2 mm sieved, air-dried soil samples were packed in plastic cylinders, closed at the bottom with a piece of cloth, and held in place with a rubber band. The plastic cylinders were 20 cm in length and 5.08 cm in internal diameter. Then, soil was weighed and added to bring the height in the cylinder to 8 cm (based on soil bulk density and the cylinder volume). The calculation was done according to the Darcy formula as follows:

$$\mathrm{K} = \frac{\mathrm{QL}}{\mathrm{HAT}}$$

Where: K = HC (cm h^{-1}), Q = volume of water conducted (cm^3), H = height of soil column (L)+ head of water (h) (cm), A = cross section area (cm^2), T = time (h)

Soil chemical analysis

The following analyses were carried out according to Burt (2014).[22]

Soil's pH

The pH was determined electrometrically in a soil paste using a pH meter.

Soil's electrical conductivity (EC)

The EC was assessed in saturated soil paste extracts using an EC meter.

Soil's cations (Na^+, K^+, Ca^{2+}, Mg^{2+})

The soluble Na^+ and K^+ were estimated photometrically by the flame photometer. Soluble Ca^{2+} and Mg^{2+} were estimated using the Versenate method and ammonium purpurate as an indicator for calcium an Eriochrome black T for calcium and magnesium.

Soil's anions (Cl^-, CO_3^{-2}, HCO_3^-, SO_4^{-2})

Chloride ions (Cl^-) was estimated by titration using 0.05 N Silver nitrate solution according to Mohr's method. Carbonate (CO_3^{-2}) and bicarbonate (HCO_3^-) were determined by titration with sulfuric acid, using the phenolphthalein and methyl orange indicators. Sulphate ions (SO_4^{-2}) were calculated by subtracting the total soluble anions from the total soluble cations.

Soil's calcium carbonate ($CaCO_3$)

Calcium Carbonate ($CaCO_3$) was determined using the Collin's Calcimeter method.

Sodium adsorption ratio (SAR)

SAR was calculated by dividing the molar concentration of the monovalent cation Na^+ by the square root of the molar concentration of the divalent cations Ca^{2+} and Mg^{2+} using the following formula:[24]

$$SAR = \frac{Na^{+1}}{\sqrt{\frac{\left(Ca^{+2}\right)+\left(Mg^{+2}\right)}{2}}}$$

Where: SAR = Sodium Adsorption Ratio, Na^+ = Water soluble Na^+ (mmol (+) L−1), Ca^{2+} = Water soluble Ca^{2+} (mmol (+) L−1), and Mg^{2+} = Water soluble Mg^{2+} (mmol (+) L−1)

Soil's cation exchange capacity (CEC)

CEC was assessed using ammonium acetate (NH_4OAc) according to Burt (2004) method.[25]

Soil's organic matter (OM)

OM was studied using the Walkley and Black method, as described by FAO (2019).[26]

Soil's gypsum content (GC)

GC was determined by acetone precipitation according to Burt's (2004) method.[25]

Soil's exchangeable sodium percentage (ESP)

ESP was calculated according to Richards *et al.* (1954) following the equation below:[27]

$$ESP = 100 * \frac{\left(-0.0126 + 0.01475\, SAR\right)}{1+\left(-0.0126 + 0.01475\, SAR\right)}$$

Physiological Analysis

Leaves of selected halophytes (*L. shawii*, *P. undulata*, and *T. niotica*) were collected from saline habitats at the flowering phase to perform several physiological tests.

Growth characters

Leaf area cm^2/ plant by the ImageJ-based method according to Cock *et al.* (2023).[28]

Chemical properties

Photosynthetic pigment

Chl content was estimated in fresh leaves as described by Witham *et al.* (1971).[29]

Antioxidant enzyme activity

a) Peroxidase activity: measured after 2 min in fresh, weighted leaves using the method described by Fehrmann and Dimond (1967).[30]
b) Phenoloxidase activity: measured after 45 min in fresh, weighted leaves that were extracted according to Hammad and Ali (2014).[31]

Proline, total carbohydrates, soluble sugars, and free amino acids (protein)

The total contents of proline, total carbohydrates and soluble sugars, and free amino acid concentrations were estimated according to the methods described by Bates et al. (1973),[32] Dubois et al. (1956),[33] and Rosen (1957),[34] respectively.

Statistical analysis

ANOVA analysis for the studied parameters was performed in SPSS (version 25; International Business Machines Corporation, NY, USA) using the least significant difference (LSD) test at the 95% significance level. Means and Standard deviation (SD) are shown.

RESULTS AND DISCUSSION

Soil physical analysis

Soil texture

The soil texture analysis at the surface (0-15 cm) and the subsurface (15-30 cm) revealed that the soil under *L. shawii* and *P. undulata* was overall moderately coarse sandy at both depths. In contrast, the soil under *T. nilotica* was fine sandy at both depths [Table 1].

Bulk density (Db)

Bulk density analysis showed the highest value in *L. shawii* at the soil's subsurface (15-30 cm) with a mean of 1.71 g cm^{-3}, whereas the surface soil (0-15 cm) for the same plant had a mean of 1.54 g cm^{-3}. On the other hand, *T. nilotica* soil surface recorded the lowest bulk density of 1.36 g cm^{-3}, and the soil subsurface for the same plant was 1.6 g cm^{-3} [Table 2].

Dp

DP analysis revealed a range of 2.36-2.54 g cm^{-3} in the surface soil and 2.59 to 2.72 g cm^{-3} in the subsurface soil. The highest values were observed in *L. shawii* soil at the soil's subsurface (15-30 cm), while the lowest values were recorded for *T. nilotica* soil at the soil's surface (0-15 cm) [Table 2].

Total porosity (P%)

The highest total porosity was found in *T. nilotica* soil, whereas *L. shawii* had the lowest. The P% of *T. nilotica* soil was 42.63% and 40.23% at the soil's surface and subsurface, respectively. Whereas *L. shawii* had a P% of 39.53% at the surface and 37.17% at the subsurface [Table 2].

HC

HC analysis showed high values of 23.33-26.33 cm h^{-1} at the soil surface and 23.67-27 cm h^{-1} at the subsurface. The lowest HC at the subsurface level was seen in *T. nilotica* soil, whereas the highest was found in *P. undulata* [Table 2].

Table 1: Physical soil analysis of the selected halophytes. Means of three sample replicates ± SD are shown.

Physical analysis*	***Particle diameter (mm)***	***P. undulata***	***T. nilotica***	***L. shawii***
Surface (0-15 cm)				
C. Sand	2-0.5	$4.87^{a} \pm 0.15$	$3.43^{b} \pm 0.42$	$4.37^{a} \pm 0.15$
M. Sand	0.5-0.1	$51.1^{a} \pm 0.53$	$35.3^{b} \pm 0.1$	$50.7^{a} \pm 0.2$
F. Sand	0.1-0.05	$41.4^{a} \pm 0.26$	$55.33^{b} \pm 0.35$	$42.7^{c} \pm 0.1$
Silt + Clay	<0.05	$2.0^{a} \pm 0.2$	$5.5^{b} \pm 0.2$	$1.9^{a} \pm 0.1$
Subsurface (15-30 cm)				
C. Sand	2-0.5	$4.2^{a} \pm 0.2$	$3.83^{b} \pm 0.15$	$3.9^{a, b} \pm 0.1$
M. Sand	0.5-0.1	$54.53^{a} \pm 0.47$	$37.37^{b} \pm 0.32$	$51.73^{c} \pm 1.16$
F. Sand	0.1-0.05	$38.5^{a} \pm 0.2$	$51.63^{b} \pm 0.25$	$40.8^{c} \pm 0.36$
Silt + Clay	<0.05	$2.93^{a} \pm 0.15$	$6.93^{b} \pm 0.4$	$2.9^{a} \pm 0.1$
Text. Class		M. Sand	F. Sand	M. Sand

*Means followed by the same letter are not significantly different at the probability level of 5% according to LSD.
C: Coarse, M: Medium, F: Fine, *P: Pulicaria, T: Tamarix, L: Lycium*

Table 2: Physical soil analysis of the selected halophytes. Means of three sample replicates ± SD are shown.

Physical properties*	***P. undulata***	***T. nilotica***	***L. shawii***
Surface (0-15 cm)			
Bulk density (Db)	1.44^{a} ± 0.03	1.36^{b} ± 0.04	1.54^{c} ± 0.04
Particle density (Dp)	2.44^{a} ± 0.04	2.36^{b} ± 0.03	2.54^{c} ± 0.05
Total porosity (P%)	$41.27^{a,\,b}$ ± 0.7	42.63^{a} ± 1.08	39.53^{b} ± 1.1
HC	$25.0^{a,\,b}$ ± 1.0	26.33^{a} ± 0.58	23.33^{b} ± 1.53
Subsurface (15-30 cm)			
Bulk density (Db)	1.6^{a} ± 0.03	1.6^{a} ± 0.04	1.71^{b} ± 0.03
Particle density (Dp)	2.59^{a} ± 0.03	2.67^{b} ± 0.02	2.72^{b} ± 0.02
Total porosity (P%)	$38.47^{a,\,b}$ ± 1.6	40.23^{a} ± 1.67	37.17^{b} ± 1.19
HC	27.0^{a} ± 1.0	23.67^{b} ± 1.53	24.33^{b} ± 0.58

*Means followed by the same letter are not significantly different at the probability level of 5% according to LSD.
Db: bulk density, Dp: particle density, P%: Porosity percentage, HC: Hydraulic conductivity.

Soil chemical analysis

pH

The pH of all selected soils was 7.8, indicating slightly alkaline soil at 25°C [Table 3].

EC

The EC analysis showed the highest EC value at the soil surface for L. shawii (1,460 ppm), whereas *P. undulata* had the lowest EC value (231.67 ppm). On the soil's subsurface 15-30 cm depth, *T. nilotica* showed the highest EC of 10,900 ppm, while *P. undulata* had the lowest 1,066.67 ppm [Table 3].

Soil cations (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+})

Cation analysis revealed that Na^{+} was the most abundant, followed by Ca2^{+}, Mg^{2+}, and K^{+}. Furthermore, Ca^{2+} concentration in *T. nilotica* was the highest at the subsurface soil (30.47 mEq L^{-1}), whereas *P. undulata* exhibited the lowest concentration (3.63 mEq L^{-1}). Mg^{2+} estimation showed the highest level in *L. shawii* at 0-15 cm depth (2.5 mEq L^{-1}), while *P. undulata* had the lowest (0.2 mEq L^{-1}). Similarly, *P. undulata* recorded the lowest at 15-30 cm depth (2.0 mEq L^{-1}), whereas *T. nilotica* showed the highest concentration of Mg^{2+} (17.93 mEq L^{-1}). K^{+} was the lowest cation among the others. *T. nilotica* soil demonstrated the highest level at subsurface, whereas *P. undulata* had the lowest at both surface and subsurface [Table 3].

Soil anions (CO_3^{-2}, HCO_3^{-}, Cl^{-}, SO_4^{-2})

Anions' analysis showed Cl^{-} had the highest level among the anions in all halophytes, followed by SO_4^{-2} and CO_3^{-2} + HCO_3^{-}, respectively. Furthermore, *L. shawii* had the highest Cl^{-} level at the soil's surface (15.27 mEq L^{-1}), whilst *T. nilotica* had the highest at the subsurface (120.13 mEq L^{-1}). On the other hand, *P. undulata* showed the lowest Cl^{-} levels at both surface and subsurface (2.5 mEq L^{-1} and 11.23 mEq L^{-1}, respectively) [Table 3].

Water sample analysis

The water sample showed a pH value of 7.16 and an EC of 112,233.3 ppm. Moreover, the soluble cations analysis showed that the soluble Na^{+} was the most abundant (1,345 mEq L^{-1}), whereas the soluble K^{+} was the lowest (21.3 mEq L^{-1}). Furthermore, Cl^{-} had the highest estimation among the soluble anions (1,480.3 mEq L^{-1}), whilst CO_3^{--}+HCO_3^{-} estimation was the lowest (23.3 mEq L^{-1}) [Table 4].

SAR

The water sample is classified as fourth class, with the highest Na^{+} content [Table 4].

Table 3: Chemical analysis of the selected halophytes' soils. Means of three sample replicates ± SD are shown.

Sample*	**pH**	**EC (ppm)**	**Soluble cations (mEq L^{-1})**				**Soluble anions (mEq L^{-1})**		
			Ca^{2+}	**Mg^{2+}**	**Na^{+}**	**K^{+}**	**CO^{3--}+ HCO^{3-}**	**Cl^{-}**	**SO^{4--}**
Surface (0-15 cm)									
P. undulata	7.82±0.02	231.67^{a}±10.41	0.6^{a}±0.1	0.2^{a}±0.1	2.87^{a}±0.15	0.14^{a}±0.03	0.11^{a}±0.01	2.5^{a}±0.2	0.8^{a}±0.1
T. nilotica	7.86±0.03	983.33^{b}±9.07	3.23^{b}±0.15	1.7^{b}±0.1	10.23^{b}±0.21	$0.18^{a,b}$±0.02	0.13^{a}±0.01	10.77^{b}±0.25	4.53^{b}±0.31
L. shawii	7.84±0.02	1460^{c}±36.06	4.33^{c}±0.15	2.5^{c}±0.1	15.0^{c}±0.2	0.3^{b}±0.1	0.22^{b}±0.03	15.27^{c}±0.25	7.13^{c}±0.15
Subsurface (15-30 cm)									
P. undulata	7.87±0.03	1066.67^{a}±30.55	3.63^{a}±0.15	2.0^{a}±0.1	10.43^{a}±0.21	0.2^{a}±0.01	0.17^{a}±0.02	11.23^{a}±0.25	4.9^{a}±0.1
T. nilotica	7.88±0.02	10900^{b}±100	30.47^{b}±0.5	17.93^{b}±0.21	116.0^{b}±0.3	4.97^{b}±0.25	0.7^{b}±0.2	120.13^{b}±0.81	48.33^{b}±0.61
L. shawii	7.85±0.01	6313.33^{c}±25.17	20.2^{c}±0.72	11.87^{c}±0.15	63.33^{c}±0.91	4.23^{c}±0.25	0.42^{c}±0.07	66.33^{c}±0.42	32.03^{c}±0.15

*Means followed by the same letter are not significantly different at the probability level of 5% according to LSD. P: Pulicaria, T: Tamarix, L: Lycium

Table 4: Chemical analysis of the water (taken from the lake in the study area). Means of three sample replicates are shown.

Sample	pH	EC (ppm)	Soluble cations (mEq L^{-1})				Soluble anions (mEq L^{-1})			SAR
			Ca^{+2}	Mg^{+2}	Na^{+}	K^{+}	CO^{3--}+HCO^{3-}	Cl^{-}	SO^{4-2}	
Water	7.16	112233.3	251.0	112.5	1345.0	21.3	23.3	1480.3	228.0	99.8

$CaCO_3$

$CaCO_3$ analysis showed the highest value in L. shawii soil surface (6.07%), whereas P. undulata had the lowest concentration (4.4%). At the soil subsurface, *T. nilotica* had the highest level (5.83%), while *P. undulata* had the lowest (4.47%) [Table 5].

CEC

CEC estimation revealed the highest value in *T. nilotica* soil subsurface (12.3 Meq/100g) and 11.27 Meq/100g at the soil surface, whereas *L. shawii* had the lowest at both depths [Table 5].

OM

OM content was relatively high in the soil of *T. nilotica*, reaching 0.83% and 0.74% at the soil surface and subsurface, respectively. Whereas the soils of the *P. undulata* and *L. shawii* showed similar OM values [Table 5].

Table 5: Chemical analysis of the selected halophytes' soils. Means of three sample replicates ± SD are shown.

Chemical properties*	*P. undulata*	*T. nilotica*	*L. shawii*
Surface (0-15 cm)			
$CaCO^3$	$4.4^a \pm 0.62$	$4.97^a \pm 0.35$	$6.07^b \pm 0.4$
CEC	$9.8^a \pm 0.3$	$11.27^b \pm 0.25$	$9.03^c \pm 0.35$
O.M	$0.42^a \pm 0.08$	$0.83^b \pm 0.07$	$0.44^a \pm 0.06$
Gypsum	$0.36^a \pm 0.02$	$0.6^b \pm 0.04$	$0.53^c \pm 0.04$
ESP	$6.57^a \pm 0.31$	$7.63^b \pm 0.25$	$7.53^b \pm 0.4$
Subsurface (15-30 cm)			
$CaCO^3$	$4.47^a \pm 0.15$	$5.83^b \pm 0.21$	$4.57^a \pm 0.35$
CEC	$10.73^a \pm 0.21$	$12.3^b \pm 0.3$	$10.17^c \pm 0.31$
O.M	$0.34^a \pm 0.06$	$0.74^b \pm 0.06$	$0.42^a \pm 0.07$
Gypsum	$0.57^a \pm 0.04$	$0.78^b \pm 0.02$	$0.66^c \pm 0.03$
ESP	$7.7^a \pm 0.26$	$9.4^b \pm 0.4$	$11.4^c \pm 0.5$

*Means followed by the same letter are not significantly different at the probability level of 5% according to LSD.

$Caco_3$: calcium carbonate, CEC: cation exchange capacity, OM: organic matter, ESP: exchangeable sodium percentage

GC

The GC analysis indicated close values, with a low range of 0.36-0.78% in the selected soils. *T. nilotica* was slightly higher than the others [Table 5].

ESP

ESP analysis showed a wide range of 6.57-7.63% at the soil surface and 7.7-11.4% at the soil subsurface in selected halophytes. The highest values were observed in *L. shawii* soil at the soil's subsurface (15-30 cm), while the lowest values were recorded for *p. undulata* soil at the soil's surface (0-15 cm) [Table 5].

Physiological analysis

Growth characters

L. shawii showed the largest leaf area compared to the other plants, with an average of 2.34 cm^2/plant. In contrast, the *T. nilotica* has the smallest leaf area, with an average of 0.66 cm^2/plant [Table 6, Figure 5].

Photosynthetic pigment

Photosynthesis pigment estimation showed that *P. undulata* had the highest Chl A and B concentrations, as well as carotene, total Chl , and the Chl/carotene ratio, compared to the others. In comparison, *L. shawii* showed the lowest in all [Table 6, Figure 6].

Antioxidants

Peroxidase enzyme estimation showed the highest in *L. shawii* (477.33 u/g fresh weight/h) and the lowest in *P. undulata* (325 u/g fresh weight/h). Additionally, *P. undulata* showed the highest in polyphenol oxidase analysis (38.94 u/g fresh weight/h), whereas *T. nilotica* had the lowest (30.72 u/g fresh weight/h) [Table 7, Figure 7].

Proline

Proline estimation demonstrated the highest level in *L. shawii* (46.66 mg/100g dry weight) and the lowest in *T. nilotica* (25.49 mg/100g dry weight) [Table 7].

Table 6: Leaf area and Chl estimation in the selected halophytes. Means ± SD for three sample replicates are shown.

Sample*	Leaf area	Chl A	Chl B	Car	T. Chl	Chl A/B	T. Chl/Car
P.	1.22^a± 0.03	3.71^a± 0.15	1.75^a± 0.94	2.19^a± 0.13	5.46^a± 1.09	2.45± 0.95	7.64^a± 1.05
T.	0.66^b± 0.08	1.04^b± 0.18	0.36^b± 0.1	0.83^b± 0.17	1.41^b± 0.27	2.94± 0.55	2.24^b± 0.42
L.	2.34^c± 0.05	0.77^b± 0.34	0.28^b± 0.11	0.44^c± 0.18	1.05^b± 0.44	2.77± 0.43	1.48^b± 0.63

*Means followed by the same letter are not significantly different at the probability level of 5% according to LSD.
P: Pulicaria undulata, T: Tamarix nilotica, L: Lycium shawii, Chl: chlorophyll, Car: carotene, T: Total

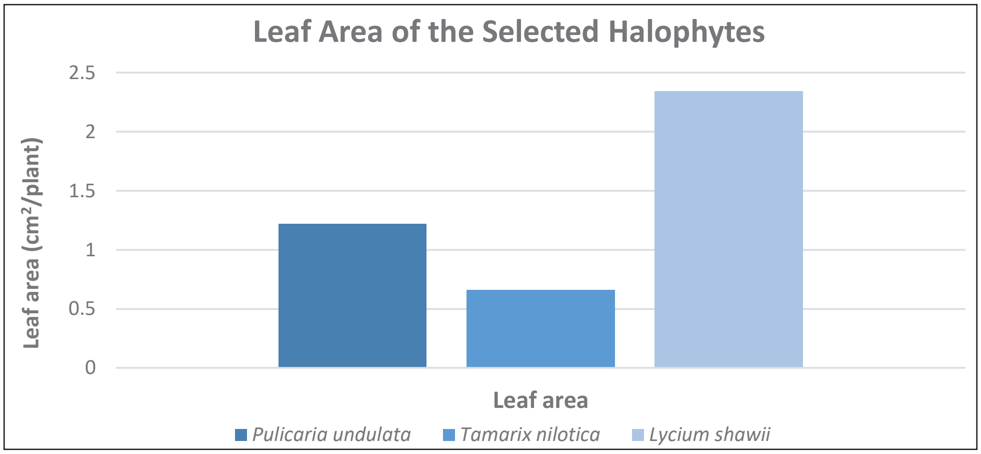

Figure 5: Estimation of leaf area of the selected halophytes. *L. shawii* had the largest leaf area of 2.34 cm^2/plant, whereas *T. nilotica* had the smallest (0.66 cm^2/plant).

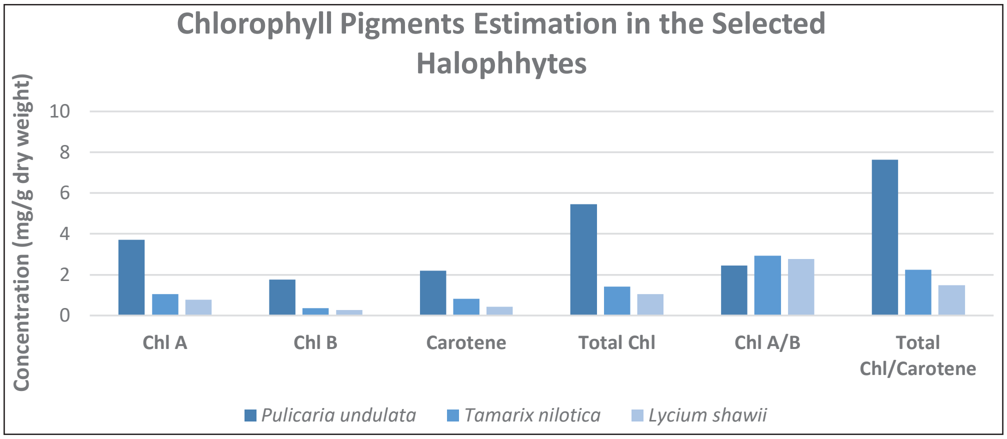

Figure 6: Estimation of Chl pigments (A and B), total Chl, and carotene in the selected halophytes. *P. undulata* had the highest concentration of Chl A, Chl B, carotene, and total Chl/carotene, while *L. shawii* had the lowest. On the other hand, *T. nilotica* had the highest Chl A/B, whereas *P. undulata* had the lowest.

Table 7: Estimation of total carbohydrates, soluble sugars, proline, protein, peroxidase, and phenoloxidase in the selected halophytes. Means of three sample replicates ± SD are shown.

Sample	Tot. carbs	TSS	Proline	Protein	Peroxidase	Phenoloxidase
P.	28.42^a± 0.11	341.17^a± 23.82	33.8^a± 3.22	13.06^a± 0.28	325.0^a± 10.15	38.94^a± 0.76
T.	31.50^b± 0.12	640.48^b± 15.03	25.49^b± 1.11	18.95^b± 0.36	419.0^b± 2.65	30.72^b± 0.94
L.	16.80^c± 0.13	278.55^c± 20.68	46.66^c± 3.0	15.41^c± 0.09	477.33^c± 9.5	36.48^c± 0.67

*Means followed by the same letter are not significantly different at the probability level of 5% according to LSD.
P: Pulicaria undulata, T: Tamarix nilotica, L: Lycium shawii, Tot. carbs: total carbohydrates, TSS: total soluble sugars.

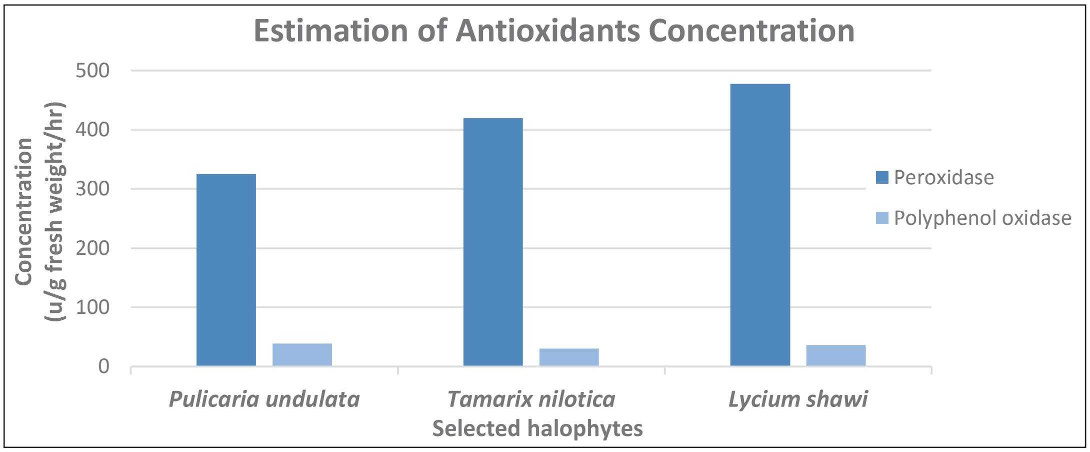

Figure 7: Estimation of antioxidant levels in the selected halophytes. *L. shawii* showed the highest concentration of peroxidase, and *P. undulata* had the lowest. However, polyphenol oxidase activity was similar among the selected halophytes, ranging from 30-38 µg fresh wt/h.

Total carbohydrates and soluble sugars

Carbohydrate estimation showed the highest content in *T. nilotica* (31.5%), while the *L. shawii* had the lowest (16.8%). Furthermore, soluble sugar analysis showed the highest value in *T. nilotica* (640.48 mg/100g dry wt), whereas *L. shawii* showed the lowest (278.55 mg/100g dry wt) [Table 7, Figure 8].

Free amino acids (Protein)

Protein analysis showed the lowest protein content in *P. undulata* (13.06%), while *T. nilotica* demonstrated the highest (18.95%) [Table 7, Figure 8].

Salinity significantly alters soil characteristics. Hence, elevated soil salt levels can lead to increased bulk density, soil compaction, compromised soil structure, clay dispersion, and the formation of surface crusts.[35] Table 1 shows that sand content is high across all soils due to the desert environment, where sandy soils are more prevalent. Moreover, the prevalence of sand contributes to soil porosity and total pore volume, allowing well-structured soil to not impose restrictions on the growth of the tested plant roots, which aligns with the soil texture investigation by Ibraheem *et al.* (2021) in selected halophytes.[36]

Db analysis showed the lowest in *T. nilotica*, which may be attributed to the soil texture under T. nilotica, which is fine sandy, and to higher total porosity. In addition, *T. nilotica* harbors a higher clay content, which also contributes to lower Db values. In contrast, the soil under *L. shawii* is moderately coarse sandy, thus exhibiting the highest Db and Dp values at both depths [Table 2]. Furthermore, P% analysis showed the highest value in *T. nilotica* soil at both depths, likely due to its soil texture and high OM and clay content. In contrast, *L. shawii* soil had the lowest P% at both depths, likely due

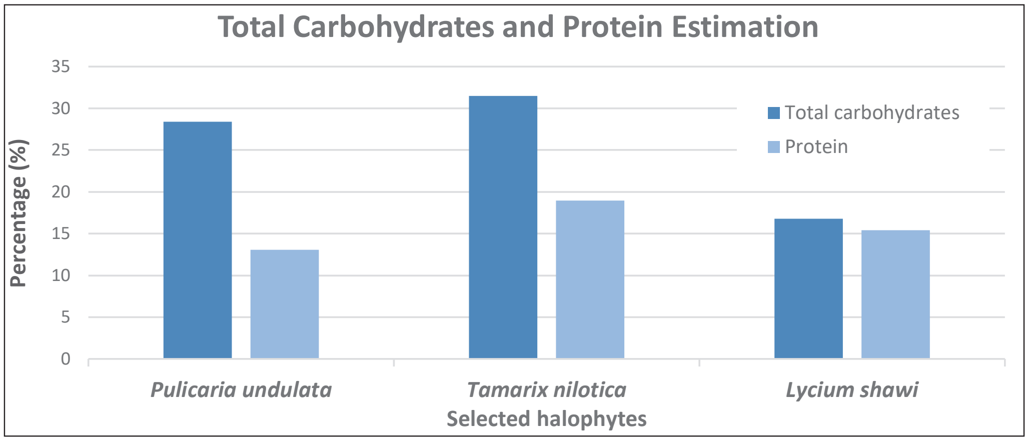

Figure 8: Estimation of total carbohydrates and protein in the selected halophytes. *T. nilotica* showed the highest estimation in both, whereas *P. undulata* had the lowest protein content, and *L. shawii* had the lowest in total carbohydrates.

to its low levels of both OM and clay content [Table 2]. According to Abd El-Wahab and Al-Salameen (2015), soil's porosity increases with a higher OM%, while it decreases with increasing soil depth; hence, at the subsurface level, due to the increased pressure from the upper layers, leading to particle compaction and reduced interstitial spaces.[37] Our OM determination showed the highest value in *T. nilotica* soil at both depths [Table 5], which is attributed to its clay and silt content. It is worth mentioning that the soil's OM content decreased as the depth increased, reflecting the presence of biological processes in the surface layer, hence making it higher in OM. Overall, the selected halophytes showed low levels of OM (below the reference range of 0.86%),[38] which may be due to rapid decomposition of OM in the soil caused by high temperatures, reduced rainfall, and increased soil aeration.[39] Similar findings by Ibraheem *et al*. (2021) were reported, in which the soil in most areas exhibited extremely low levels of organic matter, falling below the detectable limit in the selected halophytes.[36]

HC investigation revealed high values ranging from 23.33-26.33 cm h^{-1} at the soil surface and 23.67-27 cm h^{-1} at the subsurface [Table 2]. These values are generally elevated, indicating very rapid water movement, which is likely due to the overall sandy texture of the studied soils, which commonly have macropores between particles with little resistance to water movement, as well as fast drainage and low water retention. Moreover, *T. nilotica* had the lowest HC at 15-30 cm, which may be due to its fine, sandy soil and its high silt/clay ratio. Similar findings were reported by Bocuti *et al*. (2020), who found that decreased HC is affected by the high silt-clay ratio and fine particles.[40]

pH was the same for all selected halophytes and was slightly alkaline (7.8), which is attributed to the high soluble salts in saline soils [Table 3]. Similar results were reported by Ibraheem *et al*. (2022), who reported that the pH of the halophyte soil ranged from 7-8.[41]

Cation analysis showed Na^+ with the highest concentration, followed by K^+. On the other hand, anion analysis showed that Cl- had the highest concentration, and CO_2+HCO_3 had the lowest [Table 3]. Similar findings were reported by Basyoni and Aref (2016), where Na^+ was the highest among cations and Cl^- among anions in Sabkhat Jizan.[42] Furthermore, plant exposure to salinity is reported to lead to a significant rise in Na^+ and Cl^- levels in the soil, resulting in the induction of osmotic stress.[43] Moreover, EC analysis indicated variations from one depth to another for the same plant. These variations can be attributed to rainfall, which leaches excess salt from the soil and precipitates it in lower layers. Additionally, there are overall differences in EC among the soils of the studied plants. For instance, *T. nilotica* exhibited the highest at the soil's subsurface, likely due to its proximity to saline water accumulation (the lake), resulting in higher soil salinity as well as its fine sandy-textured soil. Furthermore, it may also be attributed to its high silt and clay content, which reflects a higher retention of salts in the soil. On the other hand, *P. undulata* showed the lowest EC at both depths, as it is farther from the saline water accumulation [Table 3]. Additionally, the soils of *P. undulata* and *L. shawii* are moderately coarse sandy, which results in easier *leaching* of salt by rainfall compared to fine sand.[44] Overall, all soil analyses of $CaCO_3$ were within the normal range (<8%) due to the soil's slight alkalinity (pH 7.8).[45] The water sample is classified as fourth class, with the highest Na^+ content (SAR mean of 99.8) [Table 4]. Hence, it is unsuitable for irrigation for all crops.[46]

CEC estimation showed the highest level in *T. nilotica,* which may be attributed to its high clay and OM content. Hence, the smaller the soil particles, the larger the specific surface area, and consequently, the CEC increases.[47] According to Audah and Shamsham (2008), soils with high clay and OM content generally exhibit higher CEC than sandy or low-OM soils. Furthermore, CEC is influenced by various factors, including soil texture, the quantity and type of clay minerals, OM, pH, and the soil's chemical composition. Therefore, CEC is considered an estimate of soil fertility, since exchangeable cations serve as the primary source of essential nutrients for plant growth. In addition, the GC in the selected soils ranged from 0.36-0.78%, within the expected range for sandy soils [Table 5]. Gypsum is widely distributed in arid and semi-arid regions. Gypsum crystals partially dissolve in water, with an estimated solubility of 2.6 g L^{-1}. Thus, determining the soil content of gypsum helps identify and characterize soil properties.[45]

ESP analysis showed the highest values in *T. nilotica* and *L. shawii*, due to their higher Na^+ concentrations than other cations [Table 5], as indicated by the soil chemical analysis. It's worth mentioning that there are noticeable differences in ESP between the depths of the soil for *L. shawii*. This difference is attributed to leaching of the soil surface after rainfall, leading to salt deposition in lower soil layers. Moreover, leaching of high-salt content is a good indicator that allows seeds to germinate, roots to grow, and facilitates nutrient availability for the plant.[48]

L. shawii showed the largest leaf area compared to the other plants, with an average of 2.34 cm^2/plant [Table 6, Figure 5]. Despite being subjected to considerable abiotic stress, the soil salinity beneath is estimated at EC 9.8 mΩ (6313.33 ppm) [Table 3]. In contrast, *T. nilotica* has the smallest leaf area, averaging 0.66 cm^2/plant, which can be attributed to its severe salinity stress, as the salinity level in its subsurface soil is extremely high (17 mΩ = 10900 ppm), causing the plant to reduce transpiration and water loss by minimizing leaf area [Table 6, Figure 5]. Furthermore, salt stress limits cell elongation in the growing tissue, leading to decreased leaf area and reduced dry matter assimilation in the plant. Moreover, prolonged exposure to salinity reduces photosynthesis rates, diminishes nutrient storage, and decreases growth hormone production.[43] Additionally, salt glands, such as those found in young leaves of *T. nilotica*, are also present in most halophytes,[10] serving for ion isolation due to the presence of small vacuoles in these leaves.[49]

Photosynthesis pigment estimation showed *that P. undulata* had the highest Chl A and Chl B concentration, as well as total Chl, carotene, and the Chl/carotene ratio, *w*hereas *L. shawii* showed the lowest in all. Maybe due to its less exposure to stress [Table 6, Figure 6]. Additionally, the high carotenoid content in P. undulata may have aided the protection of photosynthetic pigments by quenching singlet oxygen ($^1O_2$) and peroxyl radicals generated by excess excitation of Chl under intense light and high temperatures.[50,51] Carotenoids serve a crucial function as non-enzymatic antioxidants, protecting the photosynthetic system. Ghanem *et al*. (2021) demonstrated notable increases in carotenoid levels with elevated NaCl concentrations in selected halophytes. This upsurge in carotenoid concentration could be a strategic response to preserve Chl levels, preventing their decrease under varying salinity concentrations. Generally, saline and arid conditions significantly reduce pigment synthesis, thereby lowering the net photosynthetic rate. It is worth mentioning that *P. undulata* exhibited the lowest Chl A/B (2.45). At the same time, *T. nilotica* recorded the highest value of (2.94) [Table 6, Figure 6], which is attributed to the fact that under saline stress conditions, the plant tends to develop an increase in this ratio, which, in turn, leads to a reduction in the photosynthetic process.[18] which further confirms that *P. undulata* experiences less stress than other plants. Furthermore, Pérez-Labrada *et al*. (2019) reported that under saline stress, the plant exhibits an elevated Chl A/B ratio compared to non-stress conditions, leading to an imbalance that hinders photosynthesis.[52] In addition, photosynthesis is among the most vulnerable physiological processes to ROS induced by salinity. This susceptibility is attributed to the fact that the photosynthetic photosystem reaction centers (PSI and PSII) are the primary sites for ROS generation within chloroplasts.[53,50] Therefore, the presence of salt stress has the potential to diminish the Chl content in leaves, consequently impacting the efficiency of photosynthesis. Zhang *et al*. (2022) have reported similar observations: a decline in Chl A, B, and overall Chl content resulting from increased salt concentration.[54]

Notably, *T. nilotica* showed low Chl content, although it had the highest carbohydrate estimation. Maybe because carbohydrates can be generated independently of Chl via several metabolic processes, such as fat oxidation. *L. shawii* had the lowest Chl parameters, except for the Chl A/B ratio (which is a stress indicator), which may be attributed to its high soil salinity, which inhibits leaf photosynthetic rate and increases CO_2 concentration inside cells, thus reducing carbohydrate synthesis [Figure 8]. Additionally, TSS estimation showed the highest in *T. nilotica* and the lowest in *L. shawii*. Soluble sugars are vital in the osmotic stress response, helping plants cope with high salinity, increase water uptake, and provide nutrients for growth.[1] Similar findings were reported by Guo *et al*. (2020), who found that soluble sugar levels increased in leaves and stems after treatment with 200 mM NaCl.[55] In addition, high levels of NaCl were found to inhibit starch accumulation, thereby impacting photosynthesis. Moreover, stress-induced responses in halophytes generally involve: 1) the buildup of essential compounds (such as soluble sugars and amino acids) to resist osmotic stress and maintain cellular osmotic potential and metabolism; 2) secondary metabolites, serving as potential antioxidants and regulatory substances.[56]

Proline estimation showed the lowest in *T. nilotica* and the highest in *L. shawii* [Table 7]. Proline is reported to serve as a nitrogen source for plants during recovery phases and as a promoter of antioxidant enzyme activities. Hence, the high estimated proline level in *L. shawii* may be attributed to the high peroxidase enzyme activity. Additionally, proline levels are mediated by Ca; therefore, they may contribute to the Ca levels at the soil surface reported in the previous chemical analysis section, as well as to peroxidase.[57,58] Furthermore, plants accumulate osmotic modulators, such as proline, to maintain osmotic pressure under salt stress.[59,60] Moreover, Ghanem *et al*. (2021) have reported an increase in proline synthesis in halophytes at high salinity levels, which may be considered as a coping mechanism to compensate for the reduction in carotene and flavonoids, hence aiding the free radical scavenging activity.[18] Furthermore, protein analysis showed the highest content in *T. nilotica*, whereas *P. undulata* had the lowest [Table 7, Figure 8]. There is an inverse correlation between protein and proline content since proline is generated from protein breakdown. Therefore, we observed that *T. nilotica* had the highest protein content and the lowest proline content.[61]

Lastly, excessive ROS generation in halophytes results from salinity stress, leading to imbalances in redox reactions.[43] In addition, ROS production induces carbohydrate oxidation and pigment breakdown.[36] Therefore, we found increased levels of the antioxidant enzymes peroxidase and polyphenol oxidase to cope with elevated ROS levels [Table 7, Figure 7]. Similar results were reported by Ghanem *et al*. (2021), who found that peroxidase levels were high in halophytes, helping decrease free radical concentrations.[18]

CONCLUSION

Understanding the physiological adaptation of halophytes within the constraints imposed by these unique environmental systems is crucial for ecosystem sustainability. The selected halophytes are exposed to different salinity levels; therefore, they exhibited adaptive mechanisms such as 1) synthesis of organic osmolytes for osmotic adjustment, 2) activation of antioxidant enzymes to scavenge free radicals, which were reported in all selected halophytes, and 3) downregulation of overall metabolism to avoid oxidative stress reported in *L. shawii*, 4) reducing leaf area to minimize transpiration that was seen in *T. nilotica*, 5) Upsurge carotenoid biosynthesis for preserve Chl levels that was observed in *P. undulata*.

These results shed light on the importance of these plants as promising models for halophytes and as economically and biologically valuable, for instance, for conservation and rehabilitation of saline areas.

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