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STRUCTURAL AND FUNCTIONAL ADAPTATIONS IN *SALVADORA* SPECIES (*SALVADORA OLEOIDES* DECNE. AND *SALVADORA PERSICA* L.) FOR OPTIMAL FUNCTIONING IN SALINE ENVIRONMENTS

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Abstract

Two facultative halophytic species, *Salvadora oleoides* Decne. and *Salvadora persica* L., were collected from the highly saline region of the Salt Range located in Punjab province to evaluate their structural and functional modifications. These adaptations have evolved over a long period under saline habitat conditions. Each species demonstrated a high degree of salinity tolerance, employing distinct mechanisms for adaptation. *S. oleoides* exhibited superior salinity tolerance with enhanced growth (plant height, shoot length, leaf area) and physiological traits (high Ca^{2+} and K^+ contents, organic osmolytes, peroxidase activity and photosynthetic pigments). These features help maintain turgor, protect against oxidative stress, and support photosynthesis under high salinity. The anatomical modifications including an increased stem radius, thickened epidermis, enhanced sclerification, and increased storage tissues, as well as oil gland formation, sparse surface hairiness, and varied stomatal orientation in the leaves, collectively enhance structural support, water storage, protection against desiccation, and regulation of water loss. In contrast, the *S. persica* demonstrated higher shoot biomass (fresh and dry weight) and leaf number per shoot. Additionally, elevated leaf sodium content (Na^+), proline, and stress enzymes (superoxide dismutase and catalase), are key adaptations enabling survival under severe environmental conditions. Anatomical adaptations, such as the thickest collenchyma layer, enlarged vascular region, and reduced pith in stems, along with reduced lamina thickness, increased parenchyma in the midrib, and numerous smaller stomata in leaves, collectively enhanced structural support, water retention, and stress tolerance, supporting survival in highly saline environments. These structural and functional modifications ensure the species survival and success in challenging conditions, with implications for sustainable agriculture, ecosystem restoration, and climate change adaptation in arid and semi-arid regions.

Key words: Adaptations, Facultative halophytes, Oil glands, Storage parenchyma, Sclerification, Stomatal orientation.

Introduction

The Salt Range (coordinates 71°30'–73°30' E, 32°23'–33°00' N) is renowned for its unique topography, characterized by hilly terrain and extensive salt deposits in its rock formations. This region extends southward from the Potohar Plateau and northward to the Jhelum River. It is marked by low precipitation, with an average annual rainfall of approximately 50 cm (Hameed *et al*., 2013). The soil in the area between the Salt Range and the Jhelum River is predominantly saline, heavily influenced by the deposition of salts from brine water springs and runoff from exposed salt rocks during the rainy seasons. A significant portion of the foothill zone has become highly saline, with the soil containing up to 90% sodium chloride, along with other salts such as chlorides, carbonates, and bicarbonates of sodium, potassium, magnesium, and calcium (Qadir *et al*., 2005).

Xero-halophytes exposed to drought, salinity, and high temperatures adopt several structural and functional adaptive mechanisms. Structurally, they exhibit altered stomatal appearance and density, tapered xylem vessels, thick cuticles and epidermis, dense pubescence, large salt excretory glands, and intensive sclerification under specific environmental conditions (Iqbal *et al*., 2022-23). Functionally, they benefit from using Na^+ as a "cheap osmoticum" for turgor maintenance (Munns *et al*., 2020). Halophyte species can uptake Na^+ for their stomata regulation under hyperosmotic conditions (Rasouli *et al*., 2021). Other mechanisms include restricted ionic uptake, toxic ion efflux, ionic dilution and compartmentalization (Flowers and Colmer, 2015), and turgor maintenance via osmolyte accumulation (proline, total free amino acids, total soluble sugars, glycine betaine, and total soluble proteins) (Kumari *et al*., 2015). In response to reactive oxygen species (ROS), these plants deploy both enzymatic (guaiacol peroxidase, catalase, ascorbate peroxidase, superoxide dismutase) and non-enzymatic (ascorbic acid, α-tocopherol, carotenoids, flavonoids) defensive mechanisms, nullifying ROS through inactivation or scavenging processes (You & Chan, 2015).

Family Salvadoraceae comprising three genera (*Azima*, *Dobera*, and *Salvadora*) and ten species, is predominantly found in tropical and subtropical regions of Asia and Africa (Ishnava *et al*., 2011; Jain *et al*., 2020). The Salvadora genus, consisting of evergreen trees and shrubs, thrives in diverse habitats such as salt-affected areas, wetlands, deserts, and along riverbanks, demonstrating a wide tolerance for varying water and soil pH levels (Rangani *et al*., 2016; Nafees *et al*., 2019). These species, known as facultative halophytes, provide essential services to wildlife, including food and shelter, and act as windbreakers and soil binders in open areas (Korejo *et al*., 2010; Bhandari *et al*., 2021). In Pakistan, three Salvadora species are recognized: *Salvadora persica*, *Salvadora oleoides*, and the recently identified *Salvadora alii* (Tahir *et al*., 2010). These species exhibit strong adaptability to saline and arid environments, maintaining a high root-to-shoot ratio and deep root systems to access water in harsh conditions, while also sustaining green foliage during extreme heat (Orwa *et al*., 2009; Yadav *et al*., 2010). Their resilience contributes significantly to the local vegetation, making up about 10% of the natural habitat (Ronse De & Wanntorp, 2009; Haldhar *et al*., 2015).

The exploration of natural populations that are tolerant to high salinities is crucial for developing effective strategies for the re-vegetation and reclamation of salt-affected areas. Salt-tolerant species offer valuable insights into the adaptive mechanisms that enable survival under environmental stress (Ashraf, 2018) and can thus serve as model plants for studying these adaptations (Pessarakli & Kopec, 2009). This study focuses on evaluating the degree of salinity tolerance in two facultative halophytes, *Salvadora oleoides* and *Salvadora persica*, and identifying growth, structural, and physiological markers associated with salinity tolerance. We hypothesize that the morphological, anatomical, and physiological changes observed in these *Salvadora* species facilitate their adaptation to the highly saline conditions of the Salt Range. Given the prolonged exposure of these species to high salinity, it is anticipated that they have evolved traits that confer a robust tolerance to salt stress.

Materials and Methods

Study surveys and sampling layout: Sampling was conducted in six replicates from the six oldest standing trees (based on size and diameter) at one site during the flowering stage from March to July in 2019 and 2020. Plant samples were stored in plastic bags and immediately placed in an insulated cooler to preserve their integrity until laboratory analysis. A voucher for each sample was deposited in the Herbarium of the Department of Botany, University of Agriculture, Faisalabad. Two species of Salvadoraceae family [*Salvadora oleoides* Decne. and *Salvadora persica* L.] were collected from Khushab district in the Salt Range of Punjab, Pakistan (Fig. 1). *S. oleoides* was collected from steep hills of Chambal Sharif (pH 7.34, ECe 14.47 dS m^{-1}, Na^+ 2613.64 mg kg^{-1}, Cl^- 1422.14 mg kg^{-1}, K 136.24 mg kg^{-1}, Ca^{2+} 213.71 mg kg^{-1}), whereas *S. persica* was collected from Katha mountains (pH 6.65, ECe 17.92 dS m^{-1}, Na^+ 3034.15 mg kg^{-1}, Cl^- 2154.44 mg kg^{-1}, K 111.01 mg kg^{-1}, Ca^{2+} 153.46 mg kg^{-1}). Google earth pro (Window ver.20) software was used for coordinates of species collection sites (Table 1).

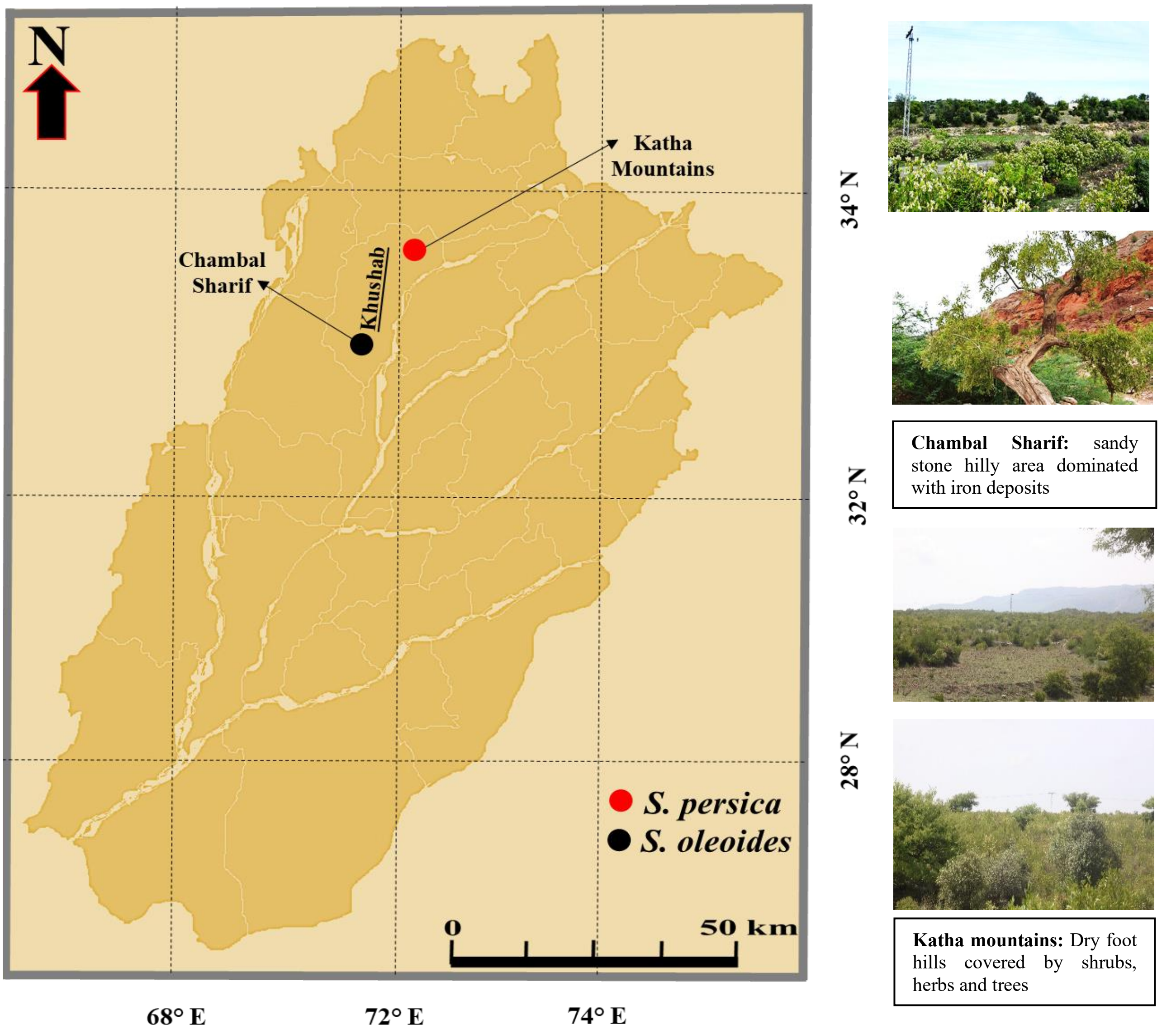

Fig. 1. Geographic distribution of *Salvadora persica* (red dot) and *Salvadora oleoides* (black dot) in Punjab, Pakistan. The map highlights key locations (Chambal Sharif and Katha Mountains) of district Khushab. Coordinates and scale are provided for spatial reference (n=6). Habitat view of the sampling sites of each species located in the Salt Range.

Physiological parameters

Soil and plant parameters: Soil samples were taken at two depths, 30 cm and 50 cm, one meter from the plant collection site.The pH/ECe meter (WTW series InoLab pH/Cond 720) was used to determine the pH and electrical conductivity (ECe). Soil extract was used to measure sodium content (Na^+) by using flame photometer (Jenway, PFP-7, Japan) and Cl^- content with the help of digital chloride ion meter (Model 926; Sherwood Scientific Ltd., Cambridge, UK). For determination of leaf ionic contents (Na^+, K^+ and Ca^{2+}), dry plant material was washed and wet grounded thoroughly into paste form by using mortar and pestle. After that paste was subjected to conc. H_2SO_4 digestion by following the method of Wolf, (1982). Finally, the reading was taken at flame photometer (Model 410, Sherwood scientific Ltd., Cambridge, Uk).

Organic osmolytes: Fresh samples were placed in Falcon tubes and stored at -80°C for later analysis of chlorophyll pigments, organic osmolytes, and antioxidants (SOD, CAT, and POD). For analysis of total soluble proteins, the method of (Lowary *et al*., 1951), glycine betaine (Grieve & Grattan, 1983), and proline content (Bates *et al*., 1973) was followed. For protein estimation, fresh leaf samples were ground in 5 mL of phosphate buffer (pH 7.0) and centrifuged for 10 minutes. The extract was then treated with an alkaline assay solution, followed by the addition of Folin reagent. After 30 minutes, the absorbance was measured at 620 nm using a UV-spectrophotometer (Hitachi-220, Japan). For glycine betaine determination, 0.5 g of fresh leaf sample was ground in 5 mL of distilled water. The filtrate was mixed with 5 mL of 2 N sulfuric acid. Then, 0.5 mL of this mixture was combined with 0.2 mL of potassium tri-iodide solution. The sample was vortexed with 2.8 mL of distilled water and 6 mL of 1,2-dichloroethane. After vortexing, the lower layer was used to measure glycine betaine concentration. For final calculation of proline contents following formulae was used:

$$Proline\ (\mu mol\ g^{-1} fresh\ weight) = \frac{\mu\text{g proline (ml}^{-1}\text{) x ml of toluene}}{\text{15.5 sample weight (g)}}$$

Antioxidants activity: To determine the antioxidants, leaf fresh material (0.5 g) was crushed by using grinder and suspended in to 50 mM ice-cooled phosphate buffer (pH 7.8). The decoction was vortexed and centrifuged, respectively. Finally, supernatant was separated to determine the antioxidant activity of catalase (CAT) and peroxidase (POD) by following the method of Chance and Mahely, (1955), while SOD activity assayed by Giannopolitis & Ries, (1977).

Photosynthetic pigments: Fresh leaf material (0.5 g) was suspended overnight in 80% acetone to extract the chlorophyll contents at room temperature (Arnon, 1949). Extract was subjected to centrifugation at 10,000 rpm for 5 min. The reading of chlorophyll a and b contents was taken at 645 and 663 nm wavelengths and carotenoids at 440.5 nm wavelength with the help of spectrophotometer (Model: hitachi-220 Japan). Following formulae were used for final values calculation:

$$Chl. a\ (mg\ g^{-1}\ f.wt.) = [12.7(\text{OD}663) - 2.69(\text{OD}645)]\text{x}\frac{\text{V}}{1000}\text{x W}]$$

$$Chl. b\ (mg\ g^{-1}\ f.wt.) = [22.9(\text{OD}645) - 4.68(\text{OD}663)]\text{x}\frac{\text{V}}{1000}\text{x W}]$$

$$Total\ chl. (mg\ g^{-1}\ f.wt.) = [20.2(\text{OD}645) - 8.02\ (\text{OD}663)]\text{x}\frac{\text{V}}{1000}\text{x W}]$$

$$Carotenoids\ (mg\ g^{-1}\ f.wt.) = [12.7(OD480) - 0.114\ (OD663)] - 0.638\ (OD645)]/2500$$

Morpho-anatomical parameters: For dry weight, samples were oven dried at 65°C until constant weight was achieved. Digital weighing balance was used for measurement of shoot fresh and dry weight, while measuring tape was used for measurement of length of topmost shoot. Clinometer was used for measurement of plant height. Morphological attributes i.e., plant height, tertiary branch length, number of leaves per shoot, total leaf area, and shoot fresh and dry weight were directly measured from fully mature plants. Morphological data recorded from three randomly selected tertiary branches originating from the lowest secondary branch of each tree were averaged and treated as a single replicate. For anatomical studies, 1.5 cm piece was taken from the middle of 2nd internode of largest branch of young stem for stem anatomy and 1.5 cm piece was excised from the center of fully matured leaf along midrib for leaf anatomy. These samples were immediately preserved in FAA (v/v 5% formalin, 10% acetic acid, 50% ethyl alcohol and 35% water) for 48 hours, and later were transferred in to acetic alcohol solution (v/v ethanol 75% and acetic acid 25%) for long term preservation. Finally, double stained (safranin and fast green) permanent slides were prepared by using free hand sectioning technique (Ruzin, 1999). Micrographs of stained sections were taken on a digital Nikon FDX-35 camera equipped with a Nikon 104 stereo-microscope. Anatomical attributes like dermal, mechanical, vascular and storage tissues were measured for leaf and stem sections. Densities of stomata and trichomes were measured per unit area (mm^2). All readings were taken with the help of ocular micrometer calibrated by stage micro-meter.

Statistical analysis

Data for all attributes were recorded in six replicates and analyzed statistically according to Steel *et al*., (1996). The LSD values were calculated for the comparison of means using MINITAB (V. 17.0) computer software. Pie chart was designed to analyze the relative proportion of studied parameters of a species by using MSXL-365 for windows (ver. 2020).

Table 1. Coordinates and habitat/nativity of *Salvadora* species collected from the Salt Range, Pakistan.

Species	Sites/Coordinates	Habitat ecology/nativity
S. oleoides Decne. (Meetha jaal)	**Chambal Sharif** "32°42'01 N" "73°25'9.99 E" Elevation: 547 m	A mesomorphic tree with drooping branches naturalize in dry regions where rainfall is extremely low. It originated from Asian countries mainly India and Pakistan and southern Iran. It is widely distributed in arid and semi-arid region of Pakistan (Khan & Qaiser, 2006)
S. persica L. (Khara jaal)	**Katha mountains** "32°34'34 N" "72°21'30 E" Elevation: 892 m	A facultative halophyte and shrubby plant with scabrous wood. It usually grows in desert and semi-desert, hilly areas, flood plains, along canal bank and saline areas. It has a wide distribution in sub-tropical and tropical region of Asia and Africa, but in Pakistan it is reported as endangered plant in Punjab except Salt Range (hilly areas) and Sindh province (Tahir *et al*., 2010)

Table 2. Morphological and physiological characteristics of *Salvadora* species collected from Salt Range, Pakistan.

Characteristics	*S. oleoides*	*S. persica*	LSD
Morphological			
Plant height (cm)	538.45a ± 29.3	484.61b ± 23.2	53.7
Shoot length (cm)	91.32a ± 6.5	77.63b ± 5.8	12.9
Number of leaves per shoot	184.13b ± 2.7	215.51a ± 6.2	27.6
Total leaf area (cm^2)	53.65a ± 4.6	42.83b ± 5.1	0.8
Shoot fresh weight (g $plant^{-1}$)	210.54b ± 6.1	262.33a ± 9.6	81.2
Shoot dry weight (g $plant^{-1}$)	105.66b ± 6.2	151.73a ± 8.3	73.4
Physiological			
Ionic content			
Shoot Na^+ (mg g^{-1} d.wt.)	32.12b ± 4.5	37.25a ± 5.1	4.8
Shoot K^+ (mg g^{-1} d.wt.)	23.45a ± 3.3	18.53b ± 2.8	3.9
Shoot Ca^{2+} (mg g^{-1} d.wt.)	40.05a ± 2.7	32.89b ± 1.3	7.6
Organic osmolytes			
Proline (µmol g^{-1} f.wt.)	15.15b ± 3.0	21.57a ± 3.2	8.9
Glycine betaine (µmol g^{-1} f.wt.)	30.33a ± 2.4	27.41b ± 1.6	2.3
Total soluble proteins (µg g^{-1} f.wt.)	75.25a ± 4.9	66.65b ± 3.0	93.8
Antioxidants			
SOD (Units µg $Protein^{-1}$)	1.22b ± 0.3	1.85a ± 0.2	0.4
CAT (Units µg $Protein^{-1}$)	1.43b ± 0.4	1.55a ± 0.5	0.2
POD (Units µg $Protein^{-1}$)	1.63a ± 0.4	1.24b ± 0.4	0.3
Photosynthetic pigments			
Chlorophyll a (mg g^{-1} f.wt.)	2.11a ± 0.6	1.73 ± 0.3	0.5
Chlorophyll b (mg g^{-1} f.wt.)	1.25a ± 0.7	0.85 ± 0.2	0.3
Carotenoids (mg g^{-1} f.wt.)	0.95a ± 0.5	0.65b ± 0.2	0.2

Means shearing similar letter in each row are not statistically significant

Results

Botanical and common descriptions of both species (*S. oleoides* and *S. persica*) along with habitat/ecology are described in (Table 1).

Growth and physiology: Both species of the *Salvadora* genus exhibited varied morpho-agronomic features (Table 2). *Salvadora oleoides* had the highest values for plant height (538.45 cm), shoot length (91.32 cm), and total leaf area (53.65 cm^2). Conversely, *Salvadora persica* had the greatest values for shoot fresh (262.33 g $plant^{-1}$) and dry weight (151.73 g $plant^{-1}$) and the number of leaves per shoot (215.51). Regarding physiological attributes, *S. oleoides* had higher concentrations of Ca^{2+} (40.05 mg g^{-1} d.wt.) and K^+ (23.45 mg g^{-1} d.wt.) in its leaves, while S. persica had the highest Na^+ content (37.25 mg g^{-1} d.wt.). *S. oleoides* also showed the maximum levels of glycine betaine (30.33 µmol g^{-1} f.wt.) and total soluble protein (75.25 µg g^{-1} f.wt.), whereas *S. persica* had higher proline content (21.57 µmol g^{-1} f.wt.). In terms of enzyme activity, *S. oleoides* exhibited higher peroxidase (POD) activity, while superoxide dismutase (SOD, 1.63 Units µg $Protein^{-1}$) and catalase (CAT) activities were higher (1.85 Units µg $Protein^{-1}$ and 1.55 Units µg $Protein^{-1}$) in *S. persica* Chlorophyll a, b and carotenoids were higher (2.11 mg g^{-1} f.wt., 1.25 mg g^{-1} f.wt. and 0.95 mg g^{-1} f.wt.) in *S. oleoides* compared to *S. persica*.

Stem anatomy: Stem anatomy revealed significant diversity in all types of tissues, including dermal, mechanical, parenchymatous, and vascular tissues. *Salvadora oleoides* had a relatively large, angular stem, whereas *Salvadora persica* had a smaller, rounded stem. *S. oleoides* featured a thick layer of epidermis with sparsely arranged trichomes on a thick cuticle. In contrast, *S. persica* had a thick epidermis surrounding a sclerified hypodermis. Large collenchymatous bundles, arranged in a ring around the central parenchymatous tissues, were observed in *S. oleoides*, while *S. persica* had a small, sclerified collenchyma layer beneath the hypodermis. *S. oleoides* also exhibited large sclerenchyma bundles arranged at regular intervals around the vascular bundles. In *S. persica*, there was a distinctive layer of sclerenchyma between the collenchyma and vascular tissues (Table 3, Fig. 2). *S. oleoides* had large vascular bundles arranged in patches with characteristically large metaxylem vessels. The phloem was divided into two parts: interxylary phloem, located inside the xylem vessels, and extraxylary phloem, located outside the xylem. In contrast, *S. persica* had distinct vascular bundles that completely encircled the pith region. These bundles contained relatively small metaxylem vessels and a smaller phloem area. The pith region in *S. oleoides* was comparatively large and flanked by vascular bundles, with prominent pith parenchyma cells that were loosely arranged with large intercellular spaces. Conversely, *S. persica* had a much reduced pith region with small, thick, and compactly arranged cells with no intercellular spaces (Table 3, Fig. 2).

Leaf anatomy: The leaf of *Salvadora oleoides* featured an oval-shaped midrib with a significant proportion of cortical parenchyma cells deposited on the adaxial surface. The leaves had a thick covering of epidermis and cuticle, along with a high density of sparsely arranged epidermal appendages, such as trichomes, and loosely arranged mesophyll parenchyma cells. Additionally, the size and density of oil glands differed between the two sides of the leaf surface; those on the abaxial surface were more conspicuous and numerous compared to the adaxial side. The vascular bundles were slightly sclerified and divided into small patches, each containing a distinct bundle of phloem on the adaxial side and a small proportion of parenchyma cells on the abaxial surface. The metaxylem vessels were relatively large and fewer in number compared to other species (Table 3, Fig. 2).

In contrast, the midrib of *Salvadora persica* leaves was arched, with a comparatively large proportion of cortical parenchyma cells surrounding the vascular region. These cells were arranged in two sections: those on the abaxial side were relatively large, loosely arranged, and had large intercellular spaces, while those on the adaxial side were small and compactly arranged. The epidermal thickness and cell area varied between the two sides of the leaf. The lower side had multilayered, thin, and large epidermal cells, whereas the upper side had single-layered, small, and thick-walled cells. The leaf exhibited reduced lamina thickness compared to other species and had small, blended mesophyll parenchyma cells. The vascular region showed a distinct proportion of phloem forming a complete ring, but the metaxylem vessels were relatively small and fewer in number compared to other species. Regarding stomatal density and area, *S. oleoides* had a high density of stomata on both sides, with the maximum stomatal area on the adaxial surface. In contrast, *S. persica* showed an increased stomatal area on the abaxial side (Table 3, Fig. 2).

Table 3. Stem and leaf anatomical characteristics of *Salvadora* species collected from Salt range, Pakistan.

Characteristics	*S. oleoides*	*S. persica*	LSD
Stem anatomy			
Stem cross sectional area (μm^2)	1669.8a ± 4.5	1228.1b ± 3.0	38.4
Epidermal thickness (μm)	12.2a ± 1.8	10.5b ± 1.2	2.1
Collenchyma thickness (μm)	13.1b ± 2.4	22.3a ± 2.8	9.8
Parenchymatous cell area (μm^2)	75.2a ± 53.5	51.3b ± 12.5	89.7
Sclerenchymatous thickness (μm)	47.2a ± 7.7	13.3b ± 1.7	33.4
Vascular bundle area (μm^2)	653.9a ± 14.8	416.4b ± 11.0	235.9
Phloem area (μm^2)	297.2a ± 8.8	286.5b ± 6.9	138.9
Metaxylem area (μm^2)	126.8a ± 4.3	121.1b ± 3.3	4.3
Pith diameter (μm)	196.9a ± 6.1	122.3b ± 14.5	66.7
Pith cell area (μm^2)	95.8a ± 7.4	78.9b ± 6.2	58.4
Leaf anatomy			
Midrib thickness (μm)	1298.8a ± 5.3	993.9b ± 3.9	5.2
Lamina thickness (μm)	161.1a ± 1.4	122.3b ± 1.6	41.6
Epidermal thickness (μm)	12.9b ± 2.0	23.6a ± 3.6	9.8
Metaxylem area (μm^2)	156.0a ± 1.9	148.2b ± 1.2	6.9
Internal oil glands area (μm^2)	300.2 ± 2.4	Absent	208.7
Vascular bundle area (μm^2)	431.4a ± 4.7	325.1b ± 3.7	567.3
Phloem area (μm^2)	205.4a ± 4.3	165.6b ± 3.3	81.5
Adaxial stomatal density (/mm^2)	90.8a ± 3.5	78.3b ± 2.8	101.8
Abaxial stomatal density (/mm^2)	74.3a ± 3.6	59.2b ± 2.6	111.3
Adaxial stomatal area (μm^2)	153.2a ± 3.3	103.3b ± 2.1	258.4
Abaxial stomatal area (μm^2)	216.2b ± 4.1	235.1a ± 3.3	479.2
Trichome density (/mm^2)	60.7a ± 3.6	57.3b ± 2.7	3.1
Trichome area (μm^2)	146.4a ± 4.7	112.9b ± 3.4	10.7

Means shearing similar letter in each row are not statistically significant

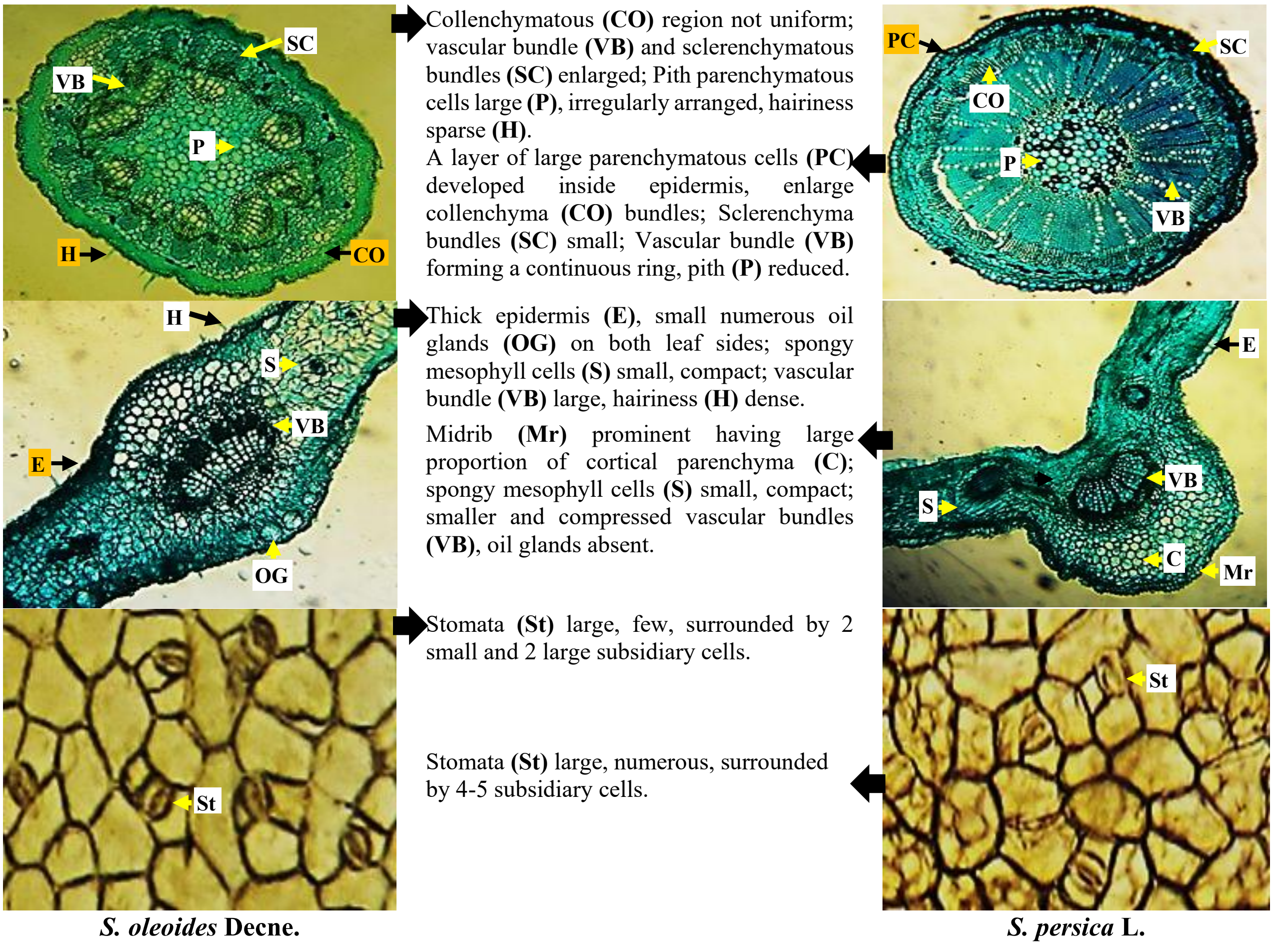

Fig. 2. Transverse sections of different parts of *Salvadora* species [*S. oleoides* Decne. and *S. persica* L.] collected from Salt Range, Pakistan (n=6, M=40X). Arrowheads indicate the specific modifications in tissues of different organs of each species.

Pie chart: Both species exhibited significantly varied relative proportions of morphological, physiological, and anatomical attributes (Fig. 3). For morphological features, *Salvadora oleoides* showed the following proportions: SF (30%), SD (28%), LN (46%), PH (52%), SL (54%), and LA (52%). In contrast, *Salvadora persica* had proportions of SW (70%), SD (72%), LN (54%), PH (48%), SL (46%), and LA (48%). Regarding physiological features, *Salvadora oleoides* had the following attributes: Chla (55%), Chlb (68%), Car (64%), Na (46%), K (54%), Ca (55%), SOD (47%), CAT (43%), POD (54%), TSP (53%), Pro (47%), and GB (61%). *Salvadora persica* exhibited the following proportions: Chla (45%), Chlb (32%), Car (36%), Na (54%), K (46%), Ca (45%), SOD (53%), CAT (57%), POD (46%), TSP (47%), Pro (53%), and GB (39%). In terms of stem anatomical attributes, *Salvadora oleoides* had proportions of ECA (54%), CoT (37%), PCA (79%), ScT (78%), VBA (35%), PhA (68%), MVA (56%), PtD (62%), and PCA (79%). *Salvadora persica* showed the following proportions: ECA (46%), CoT (63%), PCA (21%), ScT (22%), VBA (65%), PhA (32%), MVA (44%), PtD (38%), and PCA (21%). For root anatomical features, *Salvadora oleoides* had proportions of EpT (35%), MrT (50%), LMT (57%), MVA (51%), OGA (100%), VBA (34%), PhA (57%), UStD (58%), UStA (57%), LStD (69%), LStA (62%), TD (51%), and TA (67%). Conversely, *Salvadora persica* exhibited EpT (65%), MrT (50%), LMT (43%), MVA (49%), OGA (100%), VBA (66%), PhA (43%), UStD (42%), UStA (43%), LStD (31%), LStA (38%), TD (49%), and TA (33%).

Discussion

Species or populations inhabiting the Salt Range are considered to be more tolerant in terms of biomass production (Hameed and Ashraf, 2008). Due to the coexistence of various abiotic stresses, such as salinity and drought, plant communities in the Salt Range must have evolved structural and functional modifications to tolerate these highly saline conditions (Hameed *et al.*, 2013). Both *Salvadora oleoides* and *Salvadora persica* are facultative halophytes, but they differ significantly in their habits. For instance, *S. oleoides* is a tree that thrives in waterlogged areas and saline wastelands, while *S. persica* is a shrubby plant that inhabits dry and salt-affected regions. However, pure stands of both species have been recorded in their specific habitats, which are highly salt-affected.

Among growth attributes, *S. oleoides* exhibited maximum vegetative growth in terms of plant height, shoot length, and leaf area. This is a critical adaptation for plants surviving in hypersaline conditions, as they can compartmentalize toxic ions in storage parenchyma tissues, away from metabolically active tissues (Ashraf *et al*., 2018; Iqbal *et al*., 2024b). Various authors have reported similar findings in their studies on halophytic species, such as Ventura & Sagi (2013) in *Salicornia*, Vega-Galvez *et al*., (2010) in *Quinoa*, and Hanjra & Rasool (2000) in *Atriplex nummularia*. On the other hand, *S. persica* demonstrated an increase in biomass production, including shoot fresh and dry weight, and an increase in leaf numbers. Stability in biomass production of any plant species or habitat-specific population represents the degree of tolerance potential under various abiotic stresses like drought and salinity (Pessarakli *et al*., 2015).

Furthermore, in *S. oleoides*, increased uptake of beneficial ions (Ca^{2+} and K^{+}) under saline conditions is more favorable for their growth and distribution (Bhuiyan *et al*., 2015). Although high sodium concentrations in the soil can hinder the uptake of these ions, the current findings show that both species have a significant quantity of Ca^{2+} ions. This is crucial for both species' survival in hypersaline conditions (Guimarães *et al*., 2012). The accumulation of organic osmolytes (glycine betaine and soluble proteins) is another adaptive strategy of this species to prevent tissue collapse and desiccation caused by low soil water potential (Naz *et al*., 2014). Osmolytes also maintain the internal cell environment for turgor regulation and metabolic processes. High salinity can cause a significant decrease in chlorophyll content (Amareh *et al*., 2015), but the stability of photosynthetic pigments (chl a, chl b, and carotenoids) further contributes to salt tolerance in more resilient species like *S. oleoides* (Ali *et al*., 2015). Increased peroxidase (POD) activity is an offensive defensive feature of species surviving in saline environments to reduce ROS (reactive oxygen species) production and prevent oxidative stress (Flowers & Muscolo, 2015). Conversely, *S. persica* accumulated excessive amounts of sodium (Na^{+}) ions, proline, and antioxidants (SOD and CAT) in its leaves. High concentrations of Na^{+} and Cl^{-} ions were observed in plants growing under highly saline habitats, which can later cause ionic imbalances in such species (Ashraf *et al*., 2010). The high accumulation of these ions is likely when the uptake of other ions like K^{+} and Ca^{2+} is restricted due to membrane depolarization (Ashraf & Ashraf, 2012). These species may rely on the removal of toxic ions via shoots, which are also utilized in their metabolic processes (Munns & Gilliham, 2015; Kaleem *et al*., 2024). Moreover, the increased levels of proline in this species may further promote their survival rate under such harsh environmental conditions (Flowers *et al*., 2010). Salt-tolerant plants like *S. persica* typically boost antioxidant levels to prevent oxidative damage either by scavenging ROS species or by reducing their synthesis in the photosynthetic machinery (Courtney *et al*., 2016; Iqbal *et al*., 2024a).

Anatomical features relating to the stem and leaf in *Salvadora* species were not only species-specific but also indicative of their habitat ecology (Farooq *et al*., 2009). These species exhibited specific anatomical modifications that may improve water conservation under osmotic stress conditions and help them endure the impacts of various environmental challenges (Von Caemmerer & Evans, 2015; Iqbal *et al*., 2025). *S. oleoides* showed a maximum of many stem and leaf anatomical attributes, such as the proportion of dermal, mechanical, vascular, and storage tissues. Stem diameter was notably large, mainly due to the highly developed storage parenchymatous tissues (cortex and pith), mechanical, and vascular tissues (Nawaz *et al*., 2012; Hameed *et al*., 2013). All of these are vital for water conservation by either storing water within the plant, preventing tissue collapse from desiccation, or ensuring efficient water conduction from soil to aerial parts (Ahmad *et al*., 2015). The thick epidermis of the stem may also help prevent surface water loss under such extreme conditions (Konrad *et al*., 2015). Additionally, the large metaxylem and phloem areas may certainly aid in water and nutrient translocation with minimal resistance (Rayner *et al*., 2016; Iqbal *et al*., 2022). Leaf anatomy is quite responsive to climatic conditions (Iqbal *et al*., 2021). For example, *S. oleoides* exhibited thick leaves in terms of midrib and lamina thickness, intense sclerification, greater oil gland density and area, the shape and orientation of stomatal apparatus on the leaf surface, and the size of vascular bundles, particularly xylem vessels. These features highlight the succulent nature of the species, which not only enables the endurance of saline conditions through water storage but also aids in more efficient water conduction (Iqbal *et al*., 2023; Azam *et al*., 2025). The nature and density of trichomes are good indicators of the combined effects of saline and drought conditions (Grubb *et al*., 2015).

Salvadora persica possessed several pivotal features regarding stem and leaf anatomical characteristics to cope with environmental adversities such as salinity and aridity (De Micco & Aronne, 2012). The formation of a thick layer of collenchyma around the cortical tissues may protect against tissue collapse by providing additional mechanical support and maintaining tissue hydration by reducing surface water loss under extreme arid conditions (Grigore *et al*., 2014; Sarwar *et al*., 2022). Moreover, a thick epidermis on the leaf is a critical adaptation that not only protects the species from surface water loss but also reduces the direct impact of solar radiation, temperature, and wind (Chimungu *et al*., 2015; Abid *et al*., 2025). Narrow xylem vessels in this species are of vital importance, as they are less prone to collapse under water-scarce conditions (Zhaosen *et al*., 2014). Low stomatal density and area indicate the species' potential to thrive in salt-affected soils because these factors help regulate transpiration rates, which is exceptionally useful for water conservation (Camargo & Marenco, 2011; Irshad *et al*., 2024).

Fig. 3. Relative proportion of different attributes of *Salvadora* species [*S. oleoides* Decne. and *S. persica* L.] collected from the Salt Range, Pakistan (n=6, M=40X).

Abbreviations: **Figure legends: Species:** S.ol-*Salvadora oleoides,* S.pe-*Salvadora persica*; **Morphology:** SF-shoot fresh weight, SD-shoot dry weight, LN-leaf number, PH-plant height, SL-shoot length, LA-leaf area; **Physiology:** Chla-chlorophyll a, Chlb-Chlorophyll b, Car-carotenoids, Na-sodium, K-potassium, Ca-calcium, SOD-superoxide dismutase, CAT-catalase, POD-peroxidase, TSP-total soluble proteins, Pro-proline, GB-glycine betaine; **Anatomy:** ECA-epidermal cell area, CoT-cortical thickness, PCA-pith cell area, ScT-sclerenchyma thickness, VBA-vascular bundle area, PhA-phloem area, MVA-metaxylem vessel area, PtD-pith diameter, PCA-pith cell area, EpT-epidermal thickness, MrT-midrib thickness, LMT-lamina thickness, MVA-metaxylem vessel area, OGA-oil gland area, VBA-vascular bundle areas, PhA-phloem area, UStD-uper stomatal density, UStA-uper stomatal area, LStD-lower stomatal density, LStA-lower stomatal area, TD-trichome density, TA-trichome area.

Conclusion

Salvadora species (*Salvadora oleoides* and *Salvadora persica*) were found to exhibit a high degree of tolerance, allowing them to thrive in the highly saline habitats of the Salt Range in Pakistan. These species adapted through changes in growth patterns, physiological and biochemical processes, and tissue organization to sustain themselves under saline conditions. Notable adaptations included deeper root systems, strategic biomass allocation, accumulation of beneficial ions and osmolytes, enhanced photosynthetic performance, and regulatory mechanisms to manage growth and sustainance in such challenging environments. Physiological modifications helped these species overcome saline conditions and maintain tissue osmotic balance, regulate osmoregulatory processes, and inhibit the generation of reactive oxygen species. Tissue modifications included the formation of a collenchyma layer around the cortex, sclerenchyma in the vascular region, widening of xylem vessels, development of oil glands, and storage parenchyma (pith and cortex). Additionally, changes in stomatal size and orientation and the formation of trichomes were vital for these species. These adaptations provided mechanical support, efficient water translocation, additional water storage, transpiration regulation, and resistance to pathogens and herbivory. Overall, both species demonstrated significant potential for use in the rehabilitation of salt-affected areas, such as the Salt Range.

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