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Water conservation strategies through anatomical traits in the endangered arid zone species *Salvadora oleoides* Decne.

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Abstract: *Salvadora oleoides* Decne. (Salvadoraceae) is a facultative and mesomorphic xerophyte, well adapted to arid and semi-arid regions. Twelve populations were selected from different ecological regions of Punjab to investigate structural modifications that are essential for water conservation, by either improving water-storing capacity or preventing water loss from the plant body, hence, enabling this species to cope with environmental extremities. We observed significant plasticity in structural features, which ensures ecological success in a variety of environmental conditions. Huge variation was seen in various tissue systems, i.e., epidermis and epidermal appendages, collenchyma, size of internal oil glands, storage parenchyma, shape, size and arrangement of vascular tissue, intensity of sclerification, and stomatal size, shape and orientation. The desert populations showed additional parenchymatous layer under multilayered epidermis, xylem completely surrounded by phloem, broad metaxylem vessels, intensive sclerification in and outside vascular tissue, and numerous and small sized stomata on abaxial leaf surface. Population from salt-affected areas showed greater stem cross-sectional area, enlarge palisade parenchymatous cells, multilayered epidermis, large storage parenchyma, and sclerified vascular bundles. Roadside populations possessed sclerified vascular bundles and dense hairiness on leaf surface.

Key words: Oil glands, plasticity, sclerification, *Salvadora oleoides,* water conservation, xerophyte

1. Introduction

S. oleoides Decne. is a native tree of Pakistan, very well adapted to arid regions throughout the country (Bast and Kaur, 2017). It is distributed to various habitats, such as roadsides, canal and river banks, dryland salinities and saltmarshes, dry mountains, and deserts and semi-deserts. It has an excellent potential to withstand environmental extremes (Achak et al., 2018), especially aridity (Ehteshamul-Haque et al., 2013), salinity (Korejo et al., 2014) and high temperature (Barman et al., 2018). It is locally known as jall (jhaal) or pilu, which is extensively used in many folk remedies and as fuel and fodder in arid zones (Nafees et al., 2019). It is adaptable to a variety of soil and geographical conditions like saline/sodic or alkaline soils, hard rocky foothills, pure or loamy sand (Tahir et al., 2010; Shekhawat et al., 2012).

S. oleoides has become an endangered tree (regionally vulnerable) according to IUCN 2001, Red Data List Categories and Criteria due to over utilization and extensive collection (Arora et al. 2014), and therefore, has been suggested for preservation on high priority (Kumar et al. 2016). Another interesting fact about this species is its limitation to graveyards because of some religious and spiritual traditional values (Ishnava et al., 2011). People avoid cutting or eliminating this species from such areas, and this might be a strong reason of its survival in the area (Yadav et al., 2010). Although this helps the species to survive, the species′ slow growth rate and low rate of propagation are the major drawbacks.

Desert plants generally have potential to thrive prolonged drought condition and promote growth and germination, when there is availability of moisture during the season (Abd El-Ghani et al., 2017). They usually adopt their phenological and physiological mechanisms to cope with harsh environment (Tasneem et al., 2016). Phenological mechanism boosts up the plant water stress and improves the physiological adjustment by altering their structural and functional features (Rangani et al., 2018). Species like *S. oleoides* have multiple xeromorphic features like thick waxy coating on plant surface (particularly on leaves), multilayered epidermis, and abundant storage parenchyma (Tounekti et al., 2018). Other features like osmotic regulation, turgor maintenance, stomatal appearance, deep root penetration and leaf exposure (Zhang et al., 2017) also contribute significantly to survive aridity (Din et al., 2016).

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S. oleoides is known as facultative halophyte due to well adaptability under highly saline condition, and also a mesomorphic xerophyte because of maintenance of green foliage under harsh summer condition (Kumar et al., 2012). Periodically shedding of leaves is reduced by continuous supplying of water due to deep root system, which may reach up to water table (Natubhai et al., 2013). Opening of stomata on the behalf of water supply and energy dissipation is a unique feature of *Salvadora* species for lowering of leaf temperature as compared to ambient air (Yousaf and Sharif, 2013). Osmotic adjustment and water loss, reabsorption of water onset of night and water deficit are the mechanisms that contribute in drought resistance of *Salvadora* species under arid condition (Garg and Mittal, 2018).

S. oleoides is globally reported an endangered species of respective areas (Singh et al., 2013) due to its overuse by local communities. Now it has become limited towards graveyard as well as in deserts. After reviewing the status of this species, a study was aimed to evaluate its structural modification that could be useful for its future conservation. Based on broad distributional range of this species and its potential to acquire a variety of environmental conditions, it is expected that this species must have enormous plasticity in its anatomical features, so that it can adapt to wide range of climatic conditions. The present study was focused on the identification of anatomical features of aerial plant parts that may contribute towards species survival in environmental adversaries. This species is well adapted to extreme aridity, and therefore, specific anatomical modifications that contributes to xerophytic nature will be of great interest for researchers working on breeding/genetic engineering programs for increasing drought tolerance in sensitive plant species.

2. Materials and methods

A survey was conducted on different districts of Punjab province to explore the populations of *S. oleoides* (Table 1, Figure 1). A total of twelve populations were collected from ecologically distinct habitat of Punjab viz., C173-along desert canal (Rahimyar Khan), AHR-along roadside (Jhang), KHL-along railway track (Khanewal), KPR-along roadside (Rahimyar Khan), KWM-Khewra Salt Mines (Jhelum), LSR-saline desert (Bahawalpur), LYH-Thal Desert (Layyah), NWB-Cholistan Desert (Bahawalpur), RGJ-dry mountains (Dera Ghazi Khan), RUM-saline wasteland (Khushab), SSR-desert flats (Dera Ghazi Khan), TBJ-along canal bank (Muzaffargarh). Climatic data record such as annual maximum and minimum temperature was taken from substations of Meterological Department situated in each district. Global positioning system (GPS, model: Garmin E-trex 20) was used to investigate the coordinates and altitude of each site (Table 2). Five plants were collected from six different sites (each separated by at least 200 m) in each population (sample size 30 plants per population).

Five plants (of average size) were randomly selected from each study site for anatomical studies. One cm piece from the leaf center of fully matured leaf along the midrib was taken for leaf anatomy and 1 cm piece from the middle of the 2nd internode from the top of largest branch of young stem for stem anatomy were excised. Material was conserved in FAA (formaline 5%, acetic acid 10%, ethyl alcohol 50%, and distilled water 35%) solution for 48 h for fixation. Then, this material was kept under acetic alcohol solution (v/v 25% acetic acid and 75% ethyl alcohol) for a long period of conservation. Free hand sectioning was used for making of permanent slides of transverse sections of both leaf and stem by using double staining technique (safranine and fast green) as proposed by Ruzin (1999). Ocular micrometer equipped microscope was used to record data, while photographs were taken by using Carl-Zeiss (Carl Zeiss Microscopy GmbH, Oberkochen, Germany) camera equipped microscope. Six replications were used for statistical analysis.

Soil sampling was conducted 1 m away from each selected plant (5 plant) at each study site. To analyze the soil physiochemical characteristics, soil was taken at different depth level (15 and 30 cm) near the roots of plant in each habitat. A total of 200 g soil was used to prepare the saturation paste, which was used to determine the soil saturation percentage, pH value, and electrical conductivity. Saturation percentage was analyzed by subtracting the weighed value of saturated paste from actual weight of dry soil. Soil pH and ECe was recorded with the help of pH/ECe meter (WTW series InoLab pH/cond 720) by using soil extract. For determination of soil texture, we used the protocol followed by Moodie et al. (1959). Na^+, K^+, and Ca^{2+} contents were determined with a flame photometer (Jenway, PFP-7, USA), while Cl^- content was analyzed by using digital chloride ion meter (Jenway, PCLM 3).

PCA (principle correspondence analysis) was used on different soil samples and anatomical parameters to investigate the association between the sites, soil parameters and the anatomical attributes using XLSTATE (Addinsoft Inc., New York, NY, USA) software (v.20 for Windows). The data were subjected to one-way ANOVA (analysis of variance) under CRD to compare the mean values following the method of Steel et al. (1997).

3. Results

A wide range of variations were recorded in soil physiognomic characteristics of *S. oleoides* habitats. Loamy soil was observed in habitats of two populations RUM (saline wasteland) and TBJ (along canal bank); whereas,

Table 1. Ecological description and habitat view of *Salvadora oleoides* Decne. collected from different ecological regions of Punjab province.

Collection sites/District	Habitat description	Habitat view	Collection sites/ District	Habitat description	Habitat view
LSR-saline desert (Bahawalpur)	Saline patches in the Cholistan Desert, soil compact, supporting large trees of *S. oleoides*.		KHL-along railway track (Khanewal)	Dry wastelands, soil sandy clay, climate hot and dry.	
NWB-Cholistan Desert (Bahawalpur)	Small sand dunes in the Cholistan desert, climate extremely hot and dry.		RUM-saline wasteland near Warcha Salt Mines (Khushab)	Vicinity of Warcha Salt Mines, soil saline, characterized by red clay.	
RGJ-dry mountains (Dera Ghazi Khan)	Foothills of Suleman mountains, climate cool in winters and very hot in summers.		LYH-Thal Desert (Layyah)	Flats of Thal Desert, characterized by chickpea plantation on large scale.	
SSR-desert flats (Dera Ghazi Khan)	Sandy clay soil, climate very hot and dry climate.		TBJ-along canal bank (Muzaffargarh)	*S. oleoides* growing on the bank of canal, soil moist.	
AHR-along roadside (Jhang)	Sandy soil of the Thal Desert characterized by small sand dunes, climate very hot and dry.		C173-along desert canal (Rahim yar Khan)	Hot arid region characterized by sandy clay to clayey sand soil.	
KWM-Khewra Salt Mines (Jhelum)	In vicinity of salt mine, saline soil, climate dry, winters cool.		KPR-along roadside (Rahim yar Khan)	Soil is sandy loam, climate dry and hot.	

Abbreviations of the collection sites given in Table 1 were used throughout the text.

clay loamy soil was seen in habitats of two populations, i.e., LSR (saline desert) and AHR (along roadside). Loamy sand was recorded in the habitat of CC173 population, but loam to clayey loam was recorded in the habitat of KHL population (Table. 3).

Soil pH value was alkaline in nature in almost all habitats, and it was ranging from 7.7 to 9.1. Acidic pH (6.5–6.9) was noted in habitats of two populations, TBJ (along canal bank) and KPR (along roadside). Soil ECe (electrical conductivity) varied greatly in each habitat of *S. oleoides* populations, where it varied from 0.75–45 dsm^{-1}. The minimum value was seen at KPR-roadside. Habitats of two populations viz., KWM (Khewra salt mine) and RUM (saline wasteland) showed exceptionally high value of ECe than the rest of the population.

Soil Cl^- varied from 180.3–2765.5 mg L^{-1}, and the maximum value of chloride content was observed in soil of RUM population. Saturation percentage ranged from 30%–38%, and its maximum value was found in soil of RGJ population. Soil Na^+ content ranged from 88.1–4435.1 mg L^{-1} among the habitats of *S. oleoides* populations. The maximum Na^+ content was recorded in soil of saline

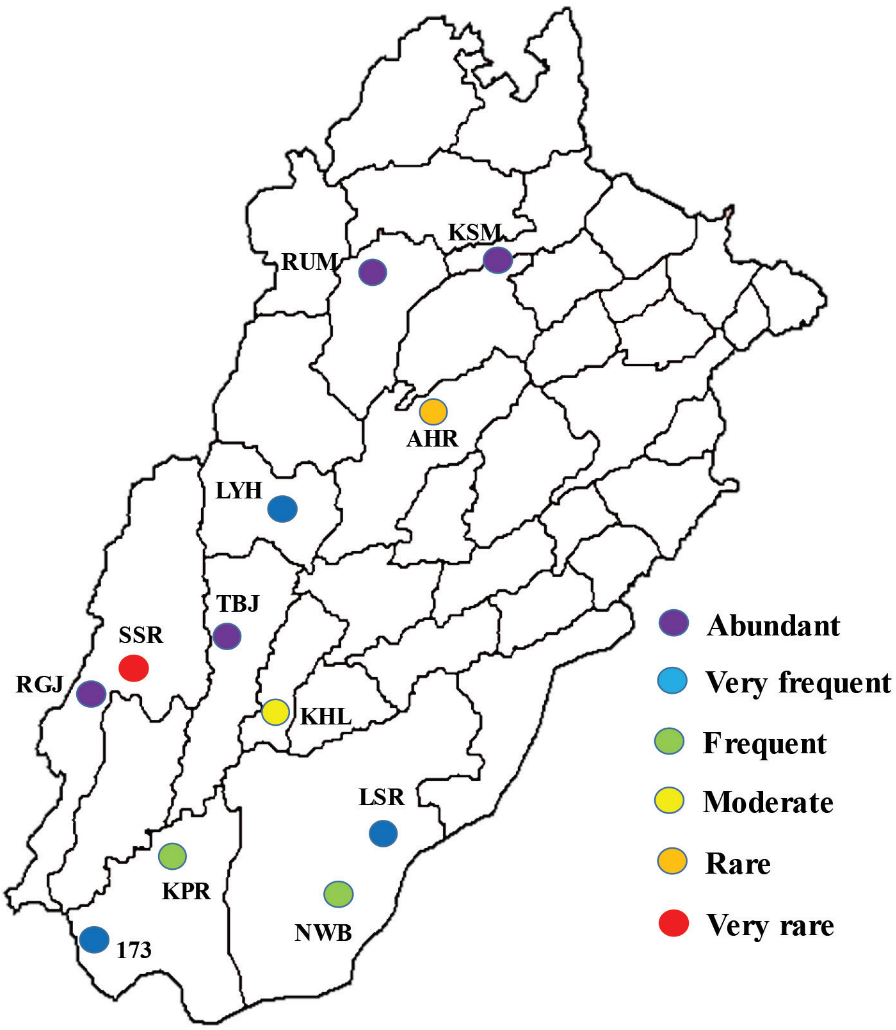


Figure 1. Map of the Punjab province showing collection sites of *Salvadora oleoides* Decne. C173-along desert canal (Rahimyar Khan), AHR-along roadside (Jhang), KHL-along railway track (Khanewal), KPR-along roadside (Rahimyar Khan), KWM-Khewra Salt Mines (Jhelum), LSR-saline desert (Bahawalpur), LYH-Thal Desert (Layyah), NWB-Cholistan Desert (Bahawalpur), RGJ-dry mountains (Dera Ghazi Khan), RUM-saline wasteland (Khushab), SSR-desert flats (Dera Ghazi Khan), TBJ-along canal bank (Muzaffargarh).

wasteland (RUM); whereas, the minimum record was observed in soil of roadside (KPR). The maximum value of soil K$^+$ was found in soil of KHL population, while the minimum value was recorded in soil of LYH population. Soil Ca^{2+} varied from 33.6–136.3 mg L^{-1}, and the highest value of this parameter was observed in soil of dry mountains population (TBJ)C173 (Table. 3).

Populations of *S. oleoides* showed very specific anatomical modifications in a variety of environmental conditions (Figure 2). Remarkable variation recorded not only in stem diameter, but also in size, nature, and shape of dermal, ground, and vascular tissue. Stem radius varied significantly in *S. oleoides* populations. The maximum (586.4 µm) of this character was recorded in saline desert population LSR (Table. 4). Its minimum (365.4 µm) was recorded in KHL population that was collected along roadside.

Epidermal thickness was the maximum (20.6 µm) in two populations, ATH and KPR, both collected along roadsides. Population SSR from flat desert and KHL along railway track showed the thinnest epidermal layer (8.1 µm). Collenchyma thickness was the maximum (83.2 µm) in populations SSR from desert flat and TBJ along canal bank. The minimum (29.3 µm) value of this parameter was

Table 2. Meterological record of *Salvadora oleoides* Decne. collected from different ecological regions of Punjab province.

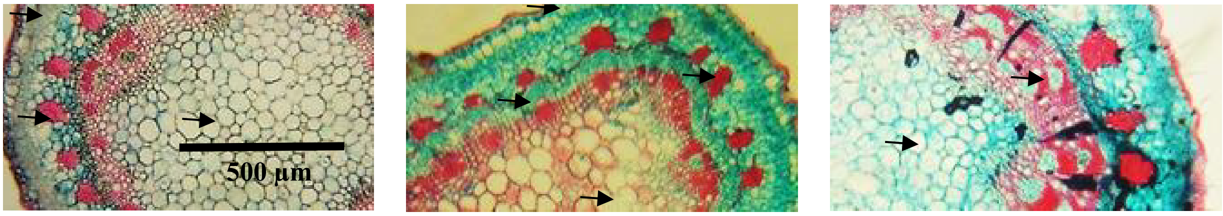
Regions	Collection sites	Habitat	Annual Temp. (°C)		Annual rainfall (mm)	Altitude m a.s.l.	Longitude (N)	Latitude (E)
			Max.	Min.				
Desert/Semi-desert	NWB	Cholistan Desert	45	10	120	98.4	28°27′ 42.58”	71°03′ 91.22″
	SSR	Flat desert	41	6	155	266.7	29°58′ 01.03”	70°19′ 36.63″
	LYH	Thal Desert	53	20	195	146.6	35°55′ 44.08”	70°56′ 31.71″
Salt affected areas	KWM	Near salt mine	40	19	237	244.4	32°37′ 59.08”	73°00′ 47.19″
	RUM	Saline wasteland	35	7	400	270.3	32°25′ 59.70”	71°56′ 41.34″
	LSR	Saline desert	41	7	236	129.2	29°25′ 43.98”	72°02′ 18.82″
Mountains	RGJ	Dry mountains	41	6	155	555.6	29°58′ 41.34”	70°81′ 58.92″
Roadside	AHR	Roadside	40	7	268	149.0`	31°10′ 43.24”	72°05′ 22.301″
	KPR	Along roadside	48	26	96	85.9	28o 37′ 46.32”	70°37′ 51.72″
	KHL	Along railway track	45	20	166	130.1	30°13′ 08.93”	71°54′ 13.29″
River/canal bank	TBJ	Along canal bank	46	25	157	133.5	30°30′ 56.44”	70°52′ 56.20″
	C173	Along Desert canal	44	6	97	75.5	28°09′ 19.29”	70°19′ 12.99″

C173-along desert canal (Rahimyar Khan), AHR-along roadside (Jhang), KHL-along railway track (Khanewal), KPR-along roadside (Rahimyar Khan), KWM-Khewra Salt Mines (Jhelum), LSR-saline desert (Bahawalpur), LYH-Thal Desert (Layyah), NWB-Cholistan Desert (Bahawalpur), RGJ-dry mountains (Dera Ghazi Khan), RUM-saline wasteland (Khushab), SSR-desert flats (Dera Ghazi Khan), TBJ-along canal bank (Muzaffargarh).

Table 3. Soil physico-chemical characteristics of *Salvadora oleoides* Decne. collected from different ecological regions of Punjab province (n = 30).

Regions	Collection sites	Soil texture	ECe (dS m^{-1})	pH	Cl^{-} (mg L^{-1})	SP	Na^{+} (mg L^{-1})	K^{+} (mg L^{-1})	Ca^{2+} (mg L^{-1})
Desert/Semi-desert	NWB	Sandy loam	1.88^{f}	8.5^{b}	180.3^{l}	30^{f}	219.5^{f}	112.1^{j}	45.6^{h}
	LYH	Sandy loam	0.99^{j}	8.1^{f}	205.7^{k}	34^{c}	121.1^{j}	58.4^{l}	89.5^{c}
	SSR	Sandy loam	1.96^{e}	7.8^{h}	245.9^{j}	32^{e}	235.8^{e}	78.4^{k}	69.8^{e}
Salt affected areas	KWM	Sandy loam	22.10^{c}	7.7^{i}	1934.1^{c}	33^{d}	2711.3^{c}	115.5^{i}	56.3^{f}
	RUM	Loam	34.15^{b}	8.3^{d}	2765.5^{a}	30^{f}	4435.1^{a}	173.5^{d}	75.5^{d}
	LSR	Clayey loam	45.22^{a}	7.9^{g}	2318.2^{b}	30^{f}	4125.7^{b}	301.7^{c}	88.5^{c}
Mountains	RGJ	Sandy loam	1.75^{g}	9.1^{a}	503.2^{e}	38^{a}	177.8^{h}	121.2^{h}	136.3^{a}
Roadside	AHR	Clayey loam	3.76^{d}	8.2^{e}	515.3^{d}	32^{e}	366.3^{d}	158.7^{e}	117.2^{b}
	KPR	Sandy loam	0.75^{l}	6.5^{k}	435.1^{g}	32^{e}	88.6^{l}	144.2^{f}	54.3^{g}
	KHL	Loam to clayey loam	1.35^{i}	8.4^{c}	410.2^{h}	32^{e}	125.7^{i}	385.9^{a}	57.9^{f}
River/canal bank	TBJ	Loam	1.51^{h}	6.9^{j}	335.8^{i}	30^{f}	198.9^{g}	371.6^{b}	88.3^{c}
	C173	Loamy sand	0.83^{k}	7.7^{i}	445.6^{f}	36^{b}	101.5^{k}	125.3^{g}	33.6^{i}

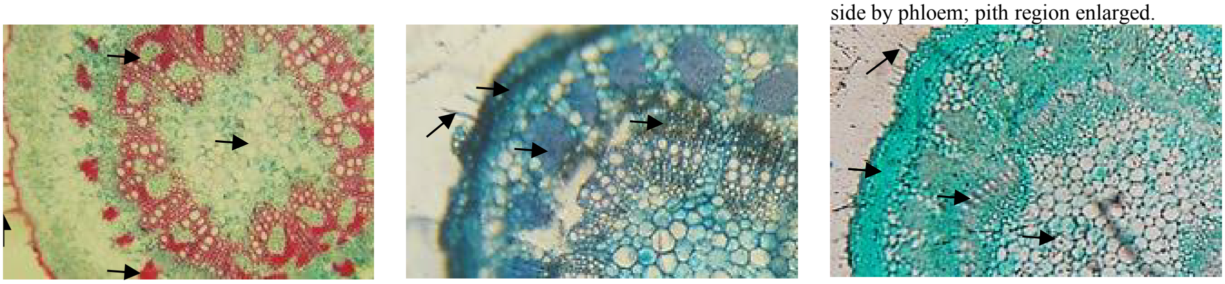
Means sharing similar letters are statistically not significant. NS: not significant, *: significant at $P > 0.05$, **: significant at $P > 0.01$, ***: significant at $P > 0.001$. C173-along desert canal (Rahimyar Khan), AHR-along roadside (Jhang), KHL-along railway track (Khanewal), KPR-along roadside (Rahimyar Khan), KWM-Khewra Salt Mines (Jhelum), LSR-saline desert (Bahawalpur), LYH-Thal Desert (Layyah), NWB-Cholistan Desert (Bahawalpur), RGJ-dry mountains (Dera Ghazi Khan), RUM-saline wasteland (Khushab), SSR-desert flats (Dera Ghazi Khan), TBJ-along canal bank (Muzaffargarh).



R-saline desert. Collenchymatous region duced; sclerenchymatous bundles small; h region enlarged, consists of loosely anged parenchyma cells.

NWB-Cholistan Desert. A later of large parenchymatous cells inside epidermis and collenchyma; Sclerenchymatous bundles small; phloem well-developed, completely surrounding xylem; pith cells enlarge.

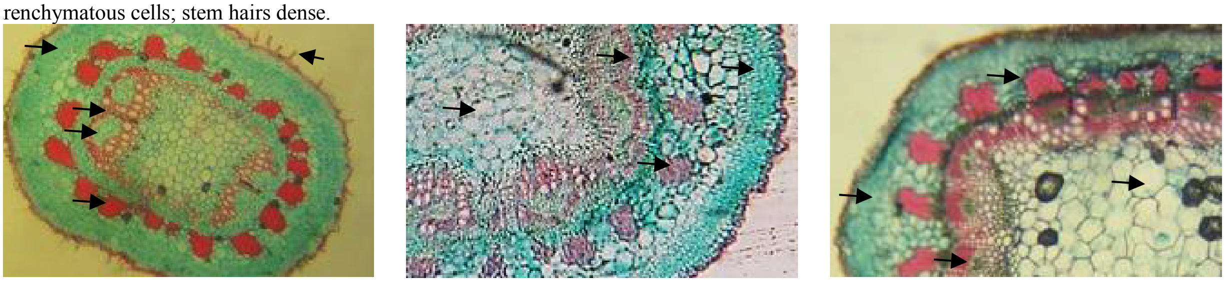
RGJ-dry mountains. Enlarged sclerenchymatous bundles; collenchymatous region reduced; vascular bundles intensively sclerified and unique, each comprising two distinct regions of xylem separated on each side by phloem; pith region enlarged.



R-desert flats. Sclerenchymatous bundle tremely reduced; vascular bundles unique ving large metaxylem area and phloem tween completely surrounded by xylem ssels; pith reduced comprising of small renchymatous cells; stem hairs dense.

AHR-along roadside. Sclerenchymatous bundles greatly enlarged; collenchyma slightly crushed; vascular bundles enlarged; stem hairs long.

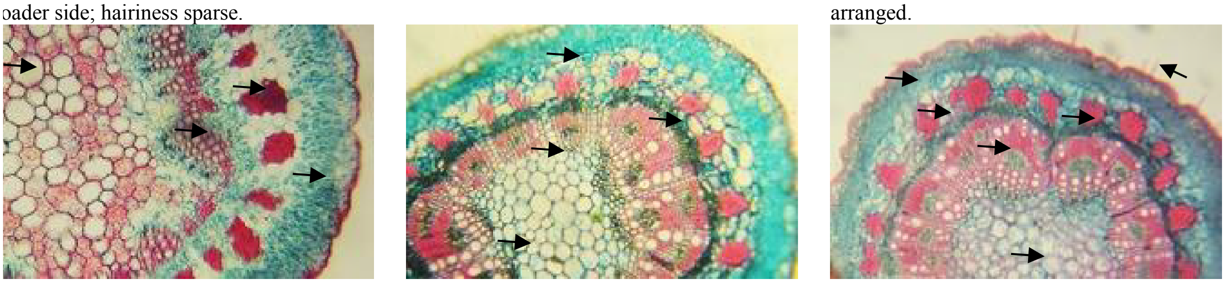
KWM-Khewra Salt Mines. Enlarged sclerenchymatous bundles, vascular bundles and collenchymatous region; compactly arranged parenchyma cells of pith; hairiness dense.



HL-along railway track. Stem cross-ctional area greatly reduced, collenchyma ll-developed, sclerenchymatous bundle all, vascular bundles more developed at oader side; hairiness sparse.

RUM-saline wasteland near Warcha Salt Mines. Enlarge collenchymatous region; sclerenchymatous bundles distinct; vascular bundles enlarged.

LYH-Thal Desert. Collenchymatous region not uniform; vascular bundle and sclerenchymatous bundles enlarged; Parenchymatous cells large, irregularly arranged.



J-along canal bank. Collenchymatous gion thick; sclerenchymatous bundles larged; large central pith comprising of larged parenchymatous cells.

C173-along desert canal. Collenchymatous region thick; sclerenchymatous bundles small; vascular bundles comprising two distinct rings, much larger on wider side.

KPR-along roadside. Sclerenchymatous bundles large. Vascular bundle forming a continuous ring, pith reduced; hairiness sparse.

Figure 2. Stem transverse sections of *Salvadora oleoides* Decne. collected from different ecological regions of Punjab province (n = 30).

Table 4. Stem anatomical characteristics of *Salvadora oleoides* Decne. collected from different ecological regions of Punjab province (n = 30, means ±SE).

	Collection	Stem radius	Epidrermal	Collenchymatous	Cortical region	Cortical cell area	Sclerenchymatous
Regions	Sites	(µm)	thickness (µm)	thickness (µm)	thickness (µm)	(µm^{2})	thickness (µm)
Desert/ Semi-desert	NWB	503.2±25.4^{d}	16.4±1.9^{b}	41.5±3.8^{e}	291.6±27.5^{b}	948.2±65.7^{d}	37.3±4.7^{h}
	LYH	503.2±22.1^{d}	16.4±1.6^{b}	58.2±6.4^{c}	312.5±24.5^{c}	1764.3±89.1^{a}	79.3±7.1^{b}
	SSR	503.2±25.4^{d}	8.1±1.1^{d}	83.2±8.1^{a}	187.4±19.4^{e}	161.9±26.7^{g}	24.8±4.7^{j}
Salt affected areas	KWM	419.6±19.3^{e}	16.4±1.9^{b}	41.5±3.8^{e}	249.9±23.6^{d}	405.4±42.3^{f}	83.2±6.3^{a}
	RUM	503.2±18.8^{d}	16.4±2.2^{b}	66.6±6.5^{b}	249.9±24.3^{d}	405.4±42.3^{f}	54.1±3.8^{e}
	LSR	586.4±29.8^{a}	12.3±1.2^{c}	41.5±3.2^{e}	312.5±27.8^{a}	975.5±65.7^{c}	49.8±8.1^{f}
Mountains	RGJ	544.7±19.3^{b}	12.3±1.2^{c}	54.1±5.0^{d}	249.9±23.6^{d}	758.1±57.9^{e}	58.2±5.6^{d}
Roadside	AHR	395.7±15.6^{f}	20.6±2.3^{a}	33.2±3.1^{f}	166.5±15.8^{f}	1220.2±76.1^{b}	83.2±9.7^{a}
	KPR	419.6±20.9^{e}	20.6±2.6^{a}	33.2±3.1^{f}	124.8±11.9^{j}	405.4±45.3^{f}	45.7±6.1^{g}
	KHL	365.4±16.3^{g}	8.1±1.1^{d}	29.3±2.7^{g}	166.5±14.1^{f}	270.1±34.5^{g}	24.8±10.1^{j}
River/canal bank	TBJ	523.8±24.0^{c}	12.3±1.5^{c}	83.2±9.7^{a}	270.8±27.2^{c}	1220.2±73.5^{b}	62.3±6.3^{c}
	C173	419.6±16.0^{e}	16.4±1.5^{b}	41.5±4.2^{e}	187.4±19.4^{e}	405.4±40.8^{f}	33.2±3.1^{i}
	F-ratio	310.0***	11.3***	261.4***	3823.0***	71.6***	313.1***
	Collection	Vascular bundle	Xylem thickness	Phloem area	Metaxylem area	Pith diameter	Pith cell area
Regions	Sites	area (µm^{2})	(µm)	(µm^{2})	(µm^{2})	(µm)	(µm^{2})
Desert/ Semi-desert	NWB	4884.5±153.1^{h}	41.4±3.8^{f}	942.8±61.4^{d}	155.1±16.3^{a}	229.3e±17.5^{e}	253.8±19.4^{f}
	LYH	5695.5±C173.9^{c}	66.4±6.5^{b}	935.9±69.9^{e}	160.2±15.7^{a}	250.2d±23.7^{d}	145.7±18.2^{g}
	SSR	6789.6±181.6^{b}	62.3±6.7^{c}	738.7±59.9^{h}	149.2±12.7^{ab}	208.5f±21.5^{f}	248.8±24.4^{f}
Salt affected areas	KWM	7812.6±193.6^{a}	58.1±6.3^{d}	1620.4±84.1^{a}	153.2±7.1^{a}	250.2±20.4^{d}	1571.5±40.3^{a}
	RUM	5535.7±165.5^{d}	41.4±5.8^{f}	401.5±41.6^{j}	139.2±14.4^{bc}	208.5±19.8^{f}	531.2±15.5^{e}
	LSR	6789.6±181.6^{b}	53.9±5.6^{e}	943.4±58.6^{d}	119.2±15.4^{c}	354.4±35.2^{a}	549.2±24.6^{d}
Mountains	RGJ	5304.7±161.4^{e}	62.3±6.1^{c}	969.1±67.7^{c}	169.2±18.6^{a}	333.6±26.5^{b}	87.9±6.2^{i}
Roadside	AHR	5688.2±191.5^{c}	74.8±6.9^{a}	671.2±56.2^{i}	159.2±14.4^{a}	250.2±25.4^{d}	708.5±29.2^{c}
	KPR	5084.6±161.6^{g}	62.3±6.1^{c}	801.9±60.1^{f}	140.2±13.4^{ab}	208.5±19.8^{f}	123.7±12.8^{h}
	KHL	2463.3±108.4^{j}	33.1±3.0^{g}	1203.1±72.4^{b}	129.2±9.7^{b}	166.8±15.9^{h}	871.1±30.6^{b}
River/canal bank	TBJ	3470.3±128.7^{i}	62.3±7.7^{c}	943.3±64.5^{d}	143.1±14.7^{ab}	271.2±24.1^{c}	91.3±9.3^{i}
	C173	5208.3±161.5^{f}	41.4±4.1^{f}	752.8±57.1^{g}	165.5±16.2^{a}	187.6±17.9^{g}	149.3±14.6^{g}
	F-ratio	75.5***	133.3***	244.2***	1.4^{NS}	1909.2***	385.5***

Means sharing similar letters are statistically not significant. NS: not significant, *: significant at $p>0.05$, **: significant at $p>0.01$, ***: significant at $p>0.001$

C173-along desert canal (Rahimyar Khan), AHR-along roadside (Jhang), KHL-along railway track (Khanewal), KPR-along roadside (Rahimyar Khan), KWM-Khewra Salt Mines (Jhelum), LSR-saline desert (Bahawalpur), LYH-Thal Desert (Layyah), NWB-Cholistan Desert (Bahawalpur), RGJ-dry mountains (Dera Ghazi Khan), RUM-saline wasteland (Khushab), SSR-desert flats (Dera Ghazi Khan), TBJ-along canal bank (Muzaffargarh).

recorded in KHL, which was collected along roadside.

Variation regarding cortical region thickness was extraordinarily high (Table 4). The maximum value (312.5 μm) was recorded in LSR and LYH population, the former collected from saline desert and the latter from Thal Desert. Population KPR along roadside showed the minimum cortical thickness (124.8 μm). In contrast, cortical cell area was the maximum in Thal Desert population LYH (1764.3 μm), but its minimum was recorded in population SSR from desert flat (161.9 μm) and KHL along railway track (270.9 μm). All populations showed huge variation in type and intensity of sclerefication. It was maximum (83.2 μm) in two populations, AHR along roadside and KWM near salt mine. Population SSR from flat desert and KHL along railway track showed the minimum sclerenchymatous thickness (24.8 μm).

Vascular bundle area was the maximum in KWM population (7812.6 μm^2), whereas its minimum was recorded in populations KHL along railway track (2463.3 μm^2) and TBJ along canal bank (3470.3 μm). Xylem thickness was the maximum in populations AHR from roadside (74.8 μm), but this parameter was the minimum in population KHL along railway track (33.1 μm). Metaxylem vessels were the broadest (169.2 μm^2) in population RGJ from dry mountains and the narrowest (119.2 μm^2) in population LSR from saline desert. Phloem area was the maximum (1620.4 μm^2) in population KWM near salt mine, and the minimum value (671.2 μm^2) was recorded in population AHR from roadside. Pith diameter was the maximum (354.4 μm) in LSR population from saline desert, while its minimum (166.8 μm) was recorded in KHL population along railway track (Table 4). Pith cell area, however, was the maximum (1571.5 μm^2) in population KWM near salt mine, but its minimum (87.9 μm^2) was in dry mountain population RGJ.

Variation in term of leaf thickness (midrib and lamina) was extremely high (Figure 3). Midrib was the thickest (420.8 μm) in two populations, RGJ, and SSR. The former was collected from dry mountains and the later from flat desert. Populations of KWM near salt mine and C173 from desert canal bank showed the thinnest leaves (270.8 μm). Lamina thickness was the maximum (354.2 μm) in dry mountain population RGJ, but it was minimum (166.5 μm) in NWB population from the Cholistan Desert. Epidermal thickness was the maximum (62.6 μm) in LSR from saline desert and the minimum (20.9 μm) of this parameter was recorded in flat desert population SSR and TBJ population along the canal bank (Table 5).

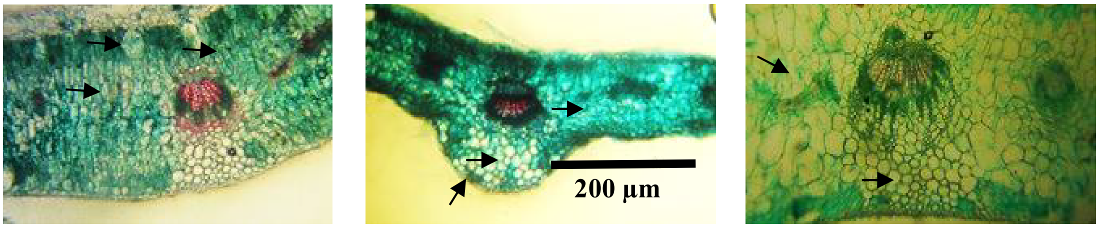
Variation regarding cortical cell area and cortical thickness was extraordinarily high in *S. oleoides* populations. Cortical cell area was the maximum (403.9 μm^2) in the Cholistan Desert population NWB and dry mountains of RGJ and it was the minimum in KPR (161.2 μm^2) and KHL (181.1 μm^2) populations, which were collected along roadside and along railway track, respectively. Populations RGJ from dry mountains showed the maximum value of cortical thickness (174.8 μm), while population KHL along railway track showed the minimum value (66.4 μm).

Metaxylem area was the maximum (120.2 μm^2) in two populations RGJ and LYH; the former was collected from dry mountains and the later from Thal Desert. Its minimum (13.8 μm^2) was observed in population KHL along railway track and TBJ along canal bank. Protoxylem area did not vary significantly in *S. oleoides* populations. The minimum value (14.5 μm^2) was recorded in four populations namely NWN (Cholistan Desert), KWM (salt mines), TBJ (along canal bank), and KPR (along roadside).

Internal oil glands were seen in many populations of *S. oleoides*. The largest glands (500.4 μm^2) were noticed in SSR population from desert flats. The minimum (166.8 μm^2) was observed in two populations: RGJ from dry mountains and TBJ along canal bank. Variation regarding vascular bundle area was significantly high. Population RGJ from dry mountains showed the maximum value (30248.4 μm^2) of this parameter, while population LSR from saline desert had the minimum value (10654.5 μm^2). Phloem area was the maximum (83.2 μm^2) in population SSR from flat desert and the minimum (41.3 μm^2) in population KPR along roadside (Table 5).

All the populations showed significant diversity in stomatal density and area (Figure 4). Stomatal density was the maximum (1031.3 per mm^2) on adaxial surface in population TBJ along canal bank. The minimum value was noted in two populations i.e., Thal Desert population LYH (486.4 per mm^2) and roadside population AHR (573.3 per mm^2). On the other hand, density was the maximum in Thal Desert population LYH on abaxial leaf surface (1014.9 per mm^2), whereas its minimum was recorded in population C173 along desert canal (372.5 per mm^2). Stomatal area was the maximum (103.1 μm^2) on adaxial surface in Cholistan Desert population NWB and minimum (46.2 μm^2) in the population LYH from Thal Desert. In opposite, stomatal area on abaxial surface was the maximum in two populations, RUM (76.8 μm^2) and LSR (74.9 μm^2), which were collected from saline wasteland and saline desert, respectively. The population TBJ along canal bank (44.8 μm^2) and RGJ from dry mountains (41.4 μm^2) had the minimum value of stomatal area on abaxial leaf surface (Table 5).

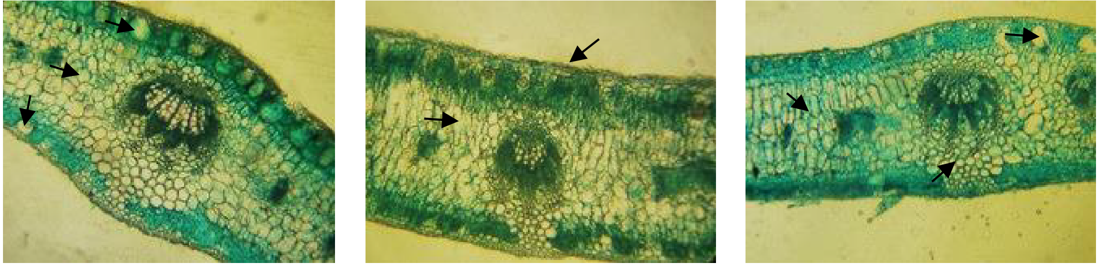
The populations of *S. oleoides* showed some peculiar modifications in response to variable environmental conditions (Figure 5). The first crucial modification in stem were size and shape of sclerids, which are brachysclerids in nature. Populations from drier habitats like Cholistan desert (NWB), desert flats (SSR), saline desert



SR-saline desert. Leaves thick; scular bundles reduced, upper idermis multilayered; palisade esophyll cells large, separated by oil ands; spongy mesophyll cells small, mpact.

NWB-Cholistan Desert. Midrib prominent having large proportion of cortical parenchyma; spongy mesophyll cells small, compact; oil glands absent.

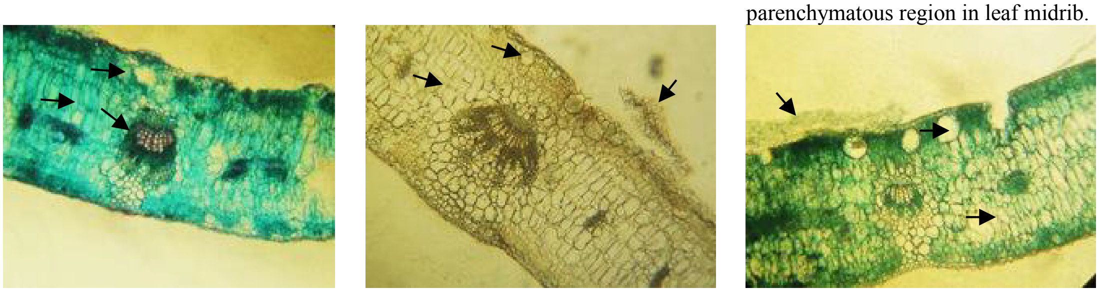
RGJ-dry mountains. Leaves extremely thick; vascular bundle much enlarged; oil glands few, small; spongy mesophyll cells large, loosly packed; cortical parenchymatous region enlarged.



R-desert flats. Small numerous oil ands on both leaf sides; spongy esophyll cells small, compact; scular bundle large.

AHR-along roadside. Oil glands absent from leaves; spongy mesophyll loosely arranged; epidermis single-layered.

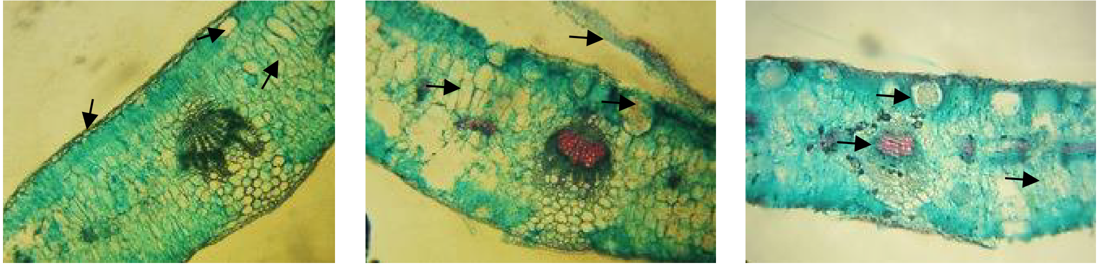
KWM-Khewra Salt Mines. Vascular bundle large; spongy mesophyll cells compactly arranged; numerous small oil glands on upper leaf surface inside epidermis; enlarged cortical parenchymatous region in leaf midrib.



HL-along railway track. Vascular ndle reduced; spongy mesophyll lls large, compact; few small oil ands inside upper epidermis.

RUM-saline wasteland near Warcha Salt Mines. Epidermis multilayered; oil glands small, few; mesophyll cells small, compact.

LYH-Thal Desert. Vascular bundles extremely reduced; oil glands numerous, small; spongy mesophyll cells large, compact; epidermis multilayered.



BJ-along canal bank. Epidermis ngle-layered; oil glands on upper leaf rface, elongated; few; spongy esophyll cells small, compact.

C173-along desert canal. Multi-layered epidermis on upper leaf surface; large oil glands inside epidermis; spongy mesophyll cells large.

KPR-along roadside. Vascular bundle extremely reduced; large oil glands on upper side inside epidermis; spongy mesophyll cells small, compact.

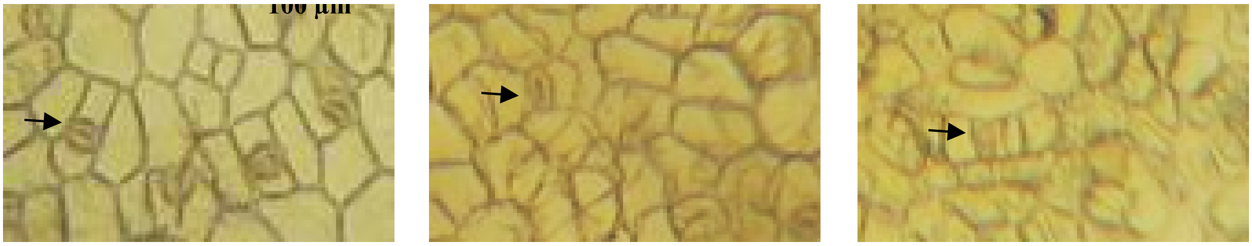
Figure 3. Leaf transverse sections of *Salvadora oleoides* Decne. collected from different ecological regions of Punjab province (n = 30).

Table 5. Leaf anatomical characteristics of *Salvadora oleoides* Decne. collected from different ecological regions of Punjab province (n = 30, means ±SE).

Regions	Collection Sites	Midrib thickness (µm)	Lamina thickness (µm)	Epidermal thickness (µm)	Cortical cell area (µm^2)	Cortical thickness (µm)	Metaxylem area (µm^2)	Protoxylem area (µm^2)
Desert/Semi-desert	NWB	250.5±10.9^{g}	166.5±14.2^{h}	29.2±3.9^{cd}	403.9±38.8^{a}	99.8d±10.3^{de}	13.8±4.4^{c}	14.5±2.1^{b}
	LYH	300.6±18.7^{d}	283.2±16.5^{e}	41.7±4.0^{b}	269.9±28.4^{c}	95.6±8.9^{e}	120.2±19.6^{a}	28.4±4.6^{a}
	SSR	354.2±18.4^{a}	299.9±21.3^{d}	20.9±2.9^{e}	268.8±23.2^{c}	133.1±13.1^{b}	53.4±10.2^{b}	27.7±3.4^{a}
Salt affected areas	KWM	270.8±13.5^{f}	258.2±9.8^{g}	33.4±4.6^{c}	322.6±22.8^{b}	112.3±11.1^{cd}	53.4±8.1^{b}	14..5±1.6^{b}
	RUM	325.2±23.7^{b}	312.4±12.9^{c}	41.7±4.1^{b}	268.9±26.4^{c}	133.1±11.4^{b}	53.4±7.1^{b}	27.7±3.7^{a}
	LSR	291.7±16.9^{d}	333.3±11.8^{b}	62.6±5.0^{a}	322.8±28.2^{b}	108.1±9.7^{d}	53.4±7.7^{b}	28.4±2.8^{a}
Mountains	RGJ	420.8±22.3^{a}	354.2±18.4^{a}	33.4±4.2^{c}	403.9±33.5^{a}	174.8±13.7^{a}	120.2±18.1^{a}	28.4±3.3^{a}
Roadside	AHR	291.7±19.9^{d}	333.3±14.8^{b}	29.2±3.9^{cd}	258.9±24.1^{c}	95.6±8.9^{e}	53.4±8.8^{b}	28.4±3.5^{a}
	KPR	308.3±11.9^{c}	266.5±10.9^{f}	25.2±3.5^{d}	161.2±16.4^{f}	91.4±9.2^{e}	53.4±8.4^{b}	14.5±2.5^{b}
	KHL	283.3±14.9^{e}	283.2±13.1^{e}	41.7±4.7^{b}	181.1±17.2^{e}	66.4±7.5^{f}	13.8±5.7^{c}	28.4±3.3^{a}
River/canal bank	TBJ	312.5±19.5^{c}	299.9±12.1^{d}	20.9±2.1^{e}	240.9±21.6^{d}	116.5±10.9^{c}	13.8±4.2^{c}	14.5±1.8^{b}
	C173	270.8±13.5^{f}	283.2±11.5^{e}	58.7±5.2^{a}	268.8±21.8^{c}	104.7±10.1^{d}	53.4±7.7^{b}	27.7±3.7^{a}
	F-ratio	698.1***	1981.2***	32.0***	3.1*	443.3***	7.2***	0.7^{NS}
Regions	Collection Sites	Internal oil glands area (µm^2)	Vascular bundle area (µm^2)	Phloem area (µm^2)	Adaxial stomatal Density per mm^2	Adaxial stomatal area (µm^2)	Abaxial stomatal density per mm^2	Abaxial stomatal area (µm^2)
Desert/Semi-desert	NWB	166.8±16.1^{e}	7608.8±374.9^{g}	62.1±6.7^{b}	647.7±19.8^{f}	103.1±10.0^{a}	732.2±20.4^{d}	53.7±7.8^{cd}
	LYH	208.5±13.7^{d}	9332.8±377.6^{f}	45.4±4.5^{f}	486.5±31.9^{j}	46.2±5.0^{f}	1014.9±26.7^{a}	49.2±4.5^{de}
	SSR	500.4±32.9^{a}	23576.2±692.6^{b}	83.2±8.0^{a}	608.1±22.2^{g}	68.2±8.3^{d}	703.3±31.5^{d}	60.8±7.3^{b}
Salt affected areas	KWM	333.6±24.3^{b}	19221.8±585.8^{d}	58.3±4.7^{c}	610.9±39.6^{g}	50.5±5.0^{e}	657.4±20.9^{e}	36.1±3.3^{h}
	RUM	208.5±17.1^{d}	20355.3±618.7^{c}	58.1±4.7^{c}	569.3±25.4^{h}	63.6±7.5^{d}	566.9±24.5^{g}	76.8±9.7^{a}
	LSR	208.5±15.9^{d}	10654.5±427.2^{g}	49.6±5.2^{e}	686.2±34.9^{e}	81.4±11.1^{b}	526.8±28.1^{g}	74.9±9.6^{a}
Mountains	RGJ	166.8±14.2^{e}	30248.4±744.4^{a}	62.1±6.1^{b}	738.3±29.0^{d}	80.2±7.8^{bc}	445.0±17.7^{h}	41.4±5.0^{g}
Roadside	AHR	250.2±20.8^{c}	18494.6±292.8^{e}	62.1±4.4^{b}	573.3±26.3^{h}	56.2±6.3^{e}	611.6±22.2^{f}	60.3±5.8^{b}
	KPR	333.5±25.2^{b}	11051.3±418.4^{c}	41.3±4.1^{g}	641.3±20.1^{f}	56.8±8.6^{e}	483.0±20.3^{i}	46.8±3.7^{ef}
	KHL	250.2±17.0^{c}	9293.4±411.4^{f}	45.4±3.9^{f}	810.3±38.7^{c}	54.3±5.8^{e}	795.7±24.3^{c}	55.1±4.6^{c}
River/canal bank	TBJ	166.8±15.9^{e}	18702.7±623.6^{e}	53.8±5.1^{d}	1031.3±42.2^{a}	76.5±7.8^{c}	984.8±29.1^{b}	44.8±5.3^{fg}
	C173	208.5±19.8^{d}	11174.5±456.2^{f}	49.6±5.2^{e}	997.8±41.3^{b}	52.4±5.3^{e}	372.5±21.9^{j}	62.6±5.4^{b}
	F-ratio	7706.8***	181.1***	76.3***	174.1***	10.1***	267.68***	6.6**

Means sharing similar letters are statistically not significant. NS: not significant, *: significant at p>0.05, **: significant at p>0.01, ***: significant at p>0.001

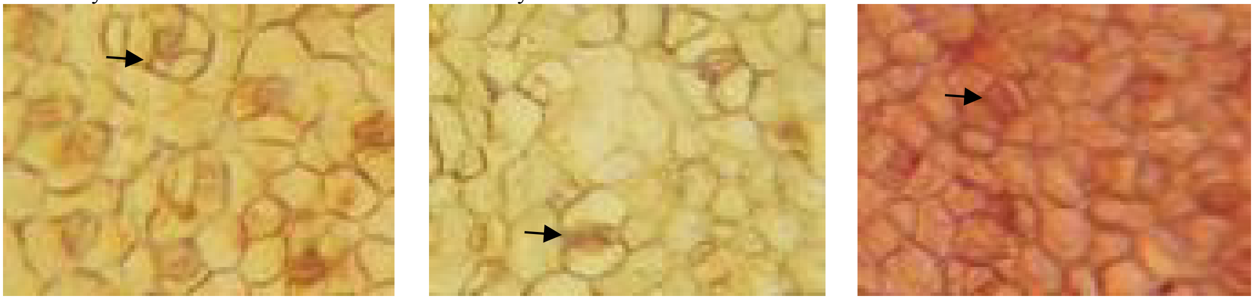
C173-along desert canal (Rahimyar Khan), AHR-along roadside (Jhang), KHL-along railway track (Khanewal), KPR-along roadside (Rahimyar Khan), KWM-Khewra Salt Mines (Jhelum), LSR-saline desert (Bahawalpur), LYH-Thal Desert (Layyah), NWB-Cholistan Desert (Bahawalpur), RGJ-dry mountains (Dera Ghazi Khan), RUM-saline wasteland (Khushab), SSR-desert flats (Dera Ghazi Khan), TBJ-along canal bank (Muzaffargarh)



LSR-saline desert. Stomata large, surrounded by 2 small and 2 large subsidiary cells.

NWB-Cholistan Desert. Stomata small, surrounded by 2 small and 2 large subsidiary cells.

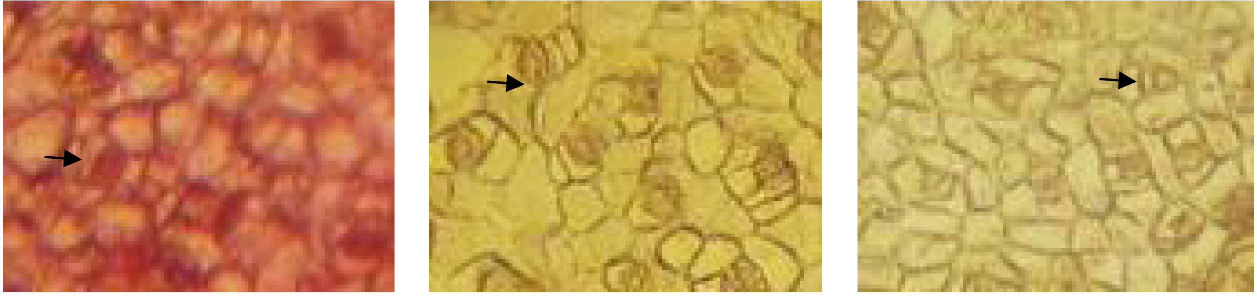
RGJ-dry mountains. Stomata large, surrounded by 4-5 subsidiary cells..



SSR-desert flats. Stomata small, surrounded by 4-5 subsidiary cells.

AHR-along roadside. Stomata large, surrounded by 4 subsidiary cells.

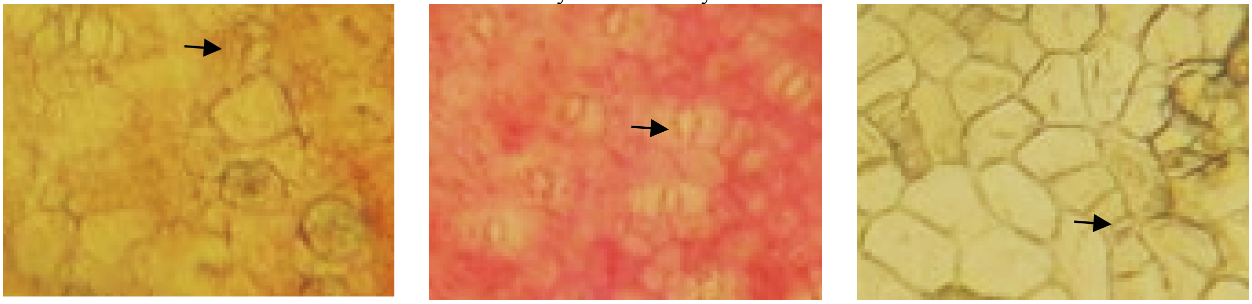
KWM-Khewra Salt Mines. Stomata surrounded by 4-5 subsidiary cells.



KHL-along railway track. Stomata small, surrounded by small subsidiary cells.

RUM-saline wasteland near Warcha Salt Mines. Stomata large, numerous, surrounded by 4-5 subsidiary cells.

LYH-Thal Desert. Stomata small, surrounded by small subsidiary cells.



TBJ-along canal bank. Stomata few, small, surrounded by 4 subsidiary cells.

C173-along desert canal. Stomata numerous, area extremely reduced.

KPR-along roadside. Stomata very few on lower leaf surface.

Figure 4. Leaf surface view of Salvadora oleoides Decne. collected from different ecological regions of Punjab province (n = 30).

Ecotype	Stem	Midrib	Leaf surface
LSR-saline desert	Pith parenchyma Water storage	Thick leaves-Multi-layered epidermis-Palisade mesophyll-Oil glands Prevention of water loss Photosynthetic activity Excretion	Large stomata Energy production
NWB-Cholistan Desert	Cortical parenchyma-Collenchyma-Phloem-Pith parenchyma Water stotage Mechanical strength Photosynthates translocation	Midrib-Cortical parenchyma Water storage	Stomata small Low transpiration rate
RGJ-dry mountains	Sclerification-Phloem-Pith parenchyma Prevention of water loss Photosynthates translocation Water storage	Thick leaves-Vascular bundles-Spongy mesophyll Cortical parenchyma Water and nutrient translocation Gaseous exchange Water storage	Stomata large Energy production
SSR-desert flats	Vascular bundles-Phloem-Hairiness Water and nutrient translocation Photosythates translocation Prevention of water loss	Oil glands-Vascular bundles Excretion Water and nutrient translocation	Stomata small Low transpiration rate
AHR-along roadside	Hairiness-Sclerification Prevention of water loss Mechanical strength	Spongy mesophyll Gaseous exchange	Large stomata Energy production
KWM-Khewra Salt Mines	Sclerification-Vascular tissue-Collenchyma-Storage parenchyma-Hairiness Prevention of water loss Water and nutrients translocation Water storage	Vascular bundles-Spongy mesophyll-Oil glands-Cortical parenchyma Water and nutrient translocation Gaseous exchange Excretion Water storage	Stomata surrounded by 4-5 subsidiary cells Stomatal regulation
KHL-along railway track	Reduction in stem diameter-Collenchyma-Vascular tissue Survival instead normal growth Mechanical strength Water and nutrients translocation	Spongy mesophyll Gaseous exchange	Stomata small Low transpiration rate
RUM-saline wasteland near Warcha Salt Mines	Collenchyma-Sclerification-Vascular tissue Mechanical strength Prevention of water loss Water and nutrient translocation	Multilayered epidermis-Mesophyll cells Prevention of water loss Photosynthetic activity	Stomata large-Numerous Energy production
LYH-Thal Desert	Vascular tissue-Sclerification-Storage parenchyma Water and nutrient translocation Prevention of water loss Water storage	Oil glands-Spongy mesophyll-Multilayered epidermis Excretion Gaseous exchange Prevention of water loss	Stomata small Low transpiration rate
TBJ-along canal bank	Collenchyma-Sclerification-Pith parenchyma Mechanical strength Prevention of water loss Water storage	Oil glands Excretion	Stomata few-Small Low transpiration rate
C173-along desert canal	Collenchyma-Vascular tissue Mechanical strength Water and nutrients translocation	Multi-layered epidermis-Oil glands-Spongy mesophyll Prevention of water loss Gaseous exchange Secretion	Stomata numerous-Area reduced Easier stomatal regulation
KPR-along roadside	Sclerification-Vascular tissue-Hairiness Prevention of water loss Mechanical strength Water and nutrients translocation	Oil glands Excretion	Stomata few Low transpiration rate

Figure 5. Block diagram showing water conservation strategies in populations of *Salvadora oleoides* Decne. collected from different ecological regions of Punjab province.

(LSR), and dry mountains (RGJ) generally had smaller sclerenchymatous area. The Thal Desert population, on the contrary, had large sclerenchymatous bundles. Population near salt mine (KWM) showed the extraordinarily large sclerenchymatous bundles.

In *S. oleoides* population, a collenchymatous layer inside epidermis is a distinctive feature. Thickness and shape, however, varies significantly among different populations. Thin layer of crushed collenchyma was seen in roadside population of AHR. In Cholistan Desert population (NWB), collenchyma was separated from epidermis by a large-celled single layer of parenchyma. Thick collenchymatous region was recorded in population C173 along desert canal, RUM from saline wasteland and TBJ along canal bank.

Size, shape and nature of vascular bundles varied significantly. Vascular bundle size varied from small (KHL along railway track) to extremely large (RUM from saline wasteland and RGJ from dry mountains). Regarding shape, some populations had one type of vascular bundle in their stem while other had small-sized to large-sized vascular bundles. In *S. oleoides,* phloem is generally on outer side of xylem. In NWB population from the Cholistan Desert, a complete ring of phloem surrounded xylem tissue. In KHL population along railway track and SSR from desert flats, phloem was observed in two distinct regions, one seen on outer side of xylem, and the other surrounded by xylem tissue. In RGJ population from dry mountains, phloem was observed on both sides of xylem tissue. Moreover, phloem was recorded in between the xylem tissues.

Two sites, RUM and LSR, showed a strong association with ECe, Cl^-, Na^+, and Ca^{2+} contents, whereas KWM showed close association with K^+ contents. Site RGJ showed close relation with saturation percentage and pH value (Fig, 6). Two sites namely WSM and AHR were strongly associated with epidermal thickness, while LYH was associated with cortical cell area. Sites RGJ and LSR were found in close association of Pith diameter and cortical thickness, respectively. TBJ showed strong impact on stem radius. RUM and SSR showed weak association with collenchyma thickness. Similarly, a weak relation of KPR site was found with phloem area and pith cell area. In case of sites verses leaf anatomical attributes association, a strong association of RUM was recorded with metaxylem and lamina thickness, whereas AHR showed with protoxylem area. Site RGJ showed weak association with midrib thickness, cortical thickness and vascular bundle area. Cortical cell area and phloem area showed association with SSR site. Abaxial stomatal density showed close association with KWM and TBJ, while adaxial stomatal density showed association with KHL site. LSR site was strongly associated with epidermal thickness and abaxial stomatal area (Figure 6).

4. Discussion

Natural populations generally show various structural modifications in response to changing environment, and regulate their growth under various stresses (Mickelbart et al., 2015; Pandey et al., 2017; Khalid et al., 2020). Xerophytes like *S. oleoides* have specific anatomical modifications to cope with adverse environmental conditions, e.g., sunken stomata, thicker epidermis, deep root system, and large proportion of water storing tissues (Bibi et al., 2015). Populations of *S. oleoides* were collected from diverse environmental conditions for the present investigation to assess plasticity in structural features that make this species adoptable to environmental heterogeneity, hence, ensuring its ecological success in extreme arid conditions. Two populations were collected from true sand deserts Cholistan (NWB) and Thal (LHY). Two populations were collected in Dera Ghazi Khan District, namely desert flats (SSR) and dry mountains (RGJ). Salt-affected areas were near Khewra Salt Mines (KWM), saline wastelands near Warcha Salt Mine (RUM) and saline desert plains at Lal Suhanra (LSR). Two populations were collected along roadside that varied in annual rainfall, i.e. relatively high precipitation at Jhang (AHR) and low precipitation at Khanpur (KPR). Two populations were from canal banks, the first with relatively higher seasonal rainfall at Muzaffargarh (TBJ) and low rainfall at Rahim Yar Khan (C173). One population was collected along railway track at Khanewal (KHL).

The Cholistan Desert population (NWB) showed some distinct modifications in its stem as well as in leaves. In stem, a single-celled parenchymatous layer inside epidermis composed of extremely large cells is an exclusive feature, not recorded in any other population. Epidermis is covered with a thick cuticle layer. The parenchymatous layer acts as a storage parenchyma that can store additional water (Liu et al., 2015; Sun et al., 2018). Therefore, survival of NWB population in extreme aridity is easier, as there is more water storage in addition to exceedingly low possibility of moisture loss through epidermal surface (Micco and Aronne, 2012). Another exceptional feature of this population is the orientation of phloem tissue. Phloem is in the form of complete ring surrounded by xylem tissue. Phloem is specific to translocation of photosynthates from leaves to other plant organs, but presence of compact phloem may certainly aid in minimizing radial movement of water from xylem tissue. Large, loosely-packed parenchymatous cells of pith can store water (Corrêa et al., 2016), which is vital for survival in longer periods of drought. Another modification in NWB population is the prominent midrib, which is again specific to this population. Proportion of storage parenchyma was high in leaf midrib, where vascular bundle is highly lignified. Such modifications are important for water conservation in NWB population, as reported by Abdel and Al-Rawi (2011).

Enlarged storage parenchyma in the Thal Desert population LYH is a peculiar modification, which guaranteed its successful survival in harsh arid environments (Al-maskri et al., 2013; Leroux et al., 2015). Large parenchymatous cells have more potential of storing water (Chen et al., 2015) and therefore, this population has more capability of withstanding longer periods of

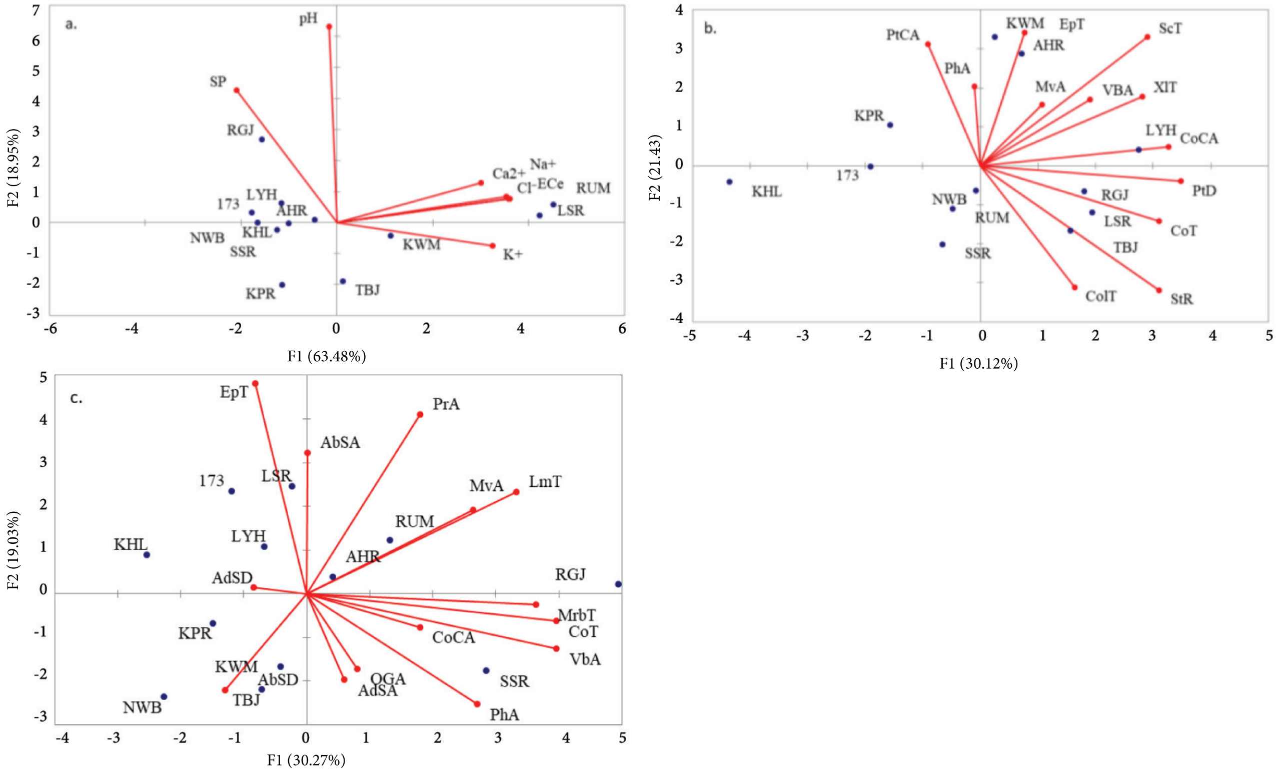


Figure 6. PCA (Principle correspondence analysis) showing biplot of a. collection sites versus soil physico-chemical characteristics and b. collection sites versus stem anatomical characteristics and c. collection sites versus leaf anatomical characteristics. **Sites:** C173-CC173, AHR- Athara Hazari, KHL- Khanewal, KPR- Khanpur, KWM-Khewra Salt Mines, LSR- Lal Sohanra, LYH- Layyah, NWB- Nawab Shah, RGJ- Rakhi Gaj, RUM- Rukhla Mandi, SSR- Sakhi Sarwar, TBJ- Taunsa Barrage. **Soil physico-chemical parameters:** PH, ECe-Electrical conductivity Na^+-Sodium, K^+-Potassium, Ca^{2+}-Calcium, Cl^--Chloride ion, SP-Saturation percentage. **Stem anatomy:** StR-Stem radius, EpT-Epidermal thickness, ColT-Collenchyma thickness, CoT-Cortical thickness, CoCA-Cortical cell area, ScT-Sclerenchyma thickness, VBA-Vascular bundle area, XlT-Xylem thickness, PhA-Phloem area, MvA-Metaxylem vessel area, PtD-Pith diameter, PtCA-Pith cell area. **Leaf anatomy:** MrbT-Midrib thickness, LmT-Lamina thickness, EpT-Epidermal thickness, CoCA-Cortical cell area, CoT-Cortical region thickness, MvA-Metaxylem vessel area, PrA-Protoxylem area, OGA-Oil glands area, VbA-Vascular bundle area, PhA-Phloem area, AdSD-Adaxial stomatal density, AdSA-Adaxial stomatal area, AbSD-Abaxial stomatal density, AbSA-Abaxial stomatal area.

water scarcity, a specific feature of deserts in Pakistan (Hameed et al., 2010). Water conservation strategies at leaf level in this population that lead to low transpiration rate were multilayered epidermis, and numerous small-sized stomata located only on abaxial leaf surface. Regulation of smaller stomata is quick and much easier (Hameed et al., 2013) and will contribute significantly in preventing water loss from leaf surface. Besides, metaxylem vessels were exceptionally large in the LYH population, which improves efficiency of water and nutrient translocation (Noman et al., 2014).

The SSR population from desert flats had explicit modifications like high proportion of collenchyma that increases mechanical strength of stem tissue (Al Hassan et al., 2015). This will protect soft delicate tissue from collapse in dry arid climatic conditions of SSR population (Naz et al., 2014; Noman et al., 2017). An enhanced area of vascular bundle and metaxylem vessels is a distinguishing feature of this population. Leaf modifications were exceptional in the SSR population. Increased succulence along with high proportion of cortical parenchyma is feature of desert vegetation that increases water storage capability significantly (Chai et al., 2013). Large vascular bundles, high proportion of phloem tissue, and enlarged oil glands are the characteristic features of this population. Oil gland size and density are often linked to leaf thickness, and therefore, indirectly contribute in water conservation (Odimegwu et al., 2013; Farooq et al., 2015)

The RGJ population from dry hot mountains depicted large sclerenchymatous layer outside vascular bundles, and heavily sclerified vascular tissue. Vascular bundles presented a rare formation, xylem in two patches surrounded on each side by phloem. Lignin deposition is a strong response of environmental stresses like aridity (Zhou et al., 2015), salinity (Alam et al., 2015), and high temperature (Rashid and Ahmed, 2011; Ola et al., 2012) where water is a limited commodity. Increased lignification in and outside vascular tissue will ensure survival in hot and dry mountainous region. Additionally, leaf modifications like thick leaves along with high proportion of mesophyll parenchymatous tissue and enlarged vascular bundles in this population will promote water and nutrient translocation (Sawidis, 2013), energy production (Toon et al., 2015), and water storage (Zhaosen et al., 2014).

The LSR population from saline desert showed a significant increase in stem cross-sectional area, which was primarily due to cortical and stem parenchyma, and vascular tissue that were with intensive sclerification. It will contribute towards increased water storage capacity as well as increased mechanical strength (Nawaz et al., 2013; Silva et al., 2014). Such modifications ensure survival of this population in hot saline and arid situations (Habib et al., 2016). Thick leaves with multilayered adaxial epidermis and large palisade mesophyll cells are a distinctive feature of this species, which are the typical feature of desert species (Claeys and Inzé, 2013). The aforementioned features will certainly increase water conservation (Hameed et al., 2012) as well as increased photosynthetic activity because larger mesophyll parenchyma must have more chloroplast organelles (Pereira et al., 2017).

The KWM population from salt-affected habitat showed high proportion of storage parenchyma, sclerified vascular tissue and chlorenchyma that can be related to better water storage capacity (Grigore et al., 2010) and mechanical strength to delicate tissues (Ogie-Odia et al., 2010). Enlarged vascular bundles in leaf and high proportion of cortical parenchyma may provide ecological fitness to survive in saline conditions (Pessarakli, 2015). Another population of salt-affected wasteland (RUM) showed similar stem and leaf architecture as the KWM population; the only significant difference was multilayered epidermis. This will improve water conservation efficiency, vital for the survival in saline habitats (Noor et al., 2015).

The roadside populations AHR and KPR had modifications like increased hairiness and sclerification, a typical feature of drought tolerant species (Mansoor et al., 2015). Increased hairiness protects plant surface from direct exposure to external environments (Naz et al., 2013) and extremely helpful in hot arid surroundings by maintaining surface temperature (Dolatabadian et al., 2011) and lowering water loss through evaporation/transpiration (Obidiegwu et al., 2015).

Increased thickness of collenchyma in stem and high density of oil glands in leaf were the distinctive features of canal bank populations TBJ and C173. This will increase mechanical strength of stem tissue (Basal, 2010; Wu et al., 2010). Besides, the TBJ population had increased sclerification and high proportion of pith parenchyma in stem, which improves water storage capacity (Geldner, 2013; Qaderi et al., 2019). The C173 population had multilayered epidermis, and this is vital for minimizing water loss from leaf surface (Correa et al., 2015). The KPR population along railway track had a significant reduction in stem diameter but increased lignification in and outside vascular tissue. This will confirm the survival in drought-prone habitats by preventing soft living tissues from collapse (Batool and Hameed, 2013) and also prevent plants from desiccation (Ashraf et al., 2012).

Leaf anatomical characteristics like leaf thickness, epidermal thickness, density and size of oil glands, arrangement of mesophyll cells, and size of vascular tissue varied significantly among the populations of *S. oleoides*. Population C173 along desert canal, saline desert population LSR, Thal Desert population LYH, and saline wasteland population RUM showed multilayered epidermis. RGJ population collected from dry mountains had the thickest leaves, which were about two-fold more than the second best. NWB population from Cholistan desert had the prominent midrib, and this type of midrib was not recorded in any other population.

Population C173 along desert canal, KPR along roadside, and LSR from Saline desert had large but few oil glands inside upper epidermis. Population KWM near salt mine, LYH from Thal Desert and RUM from saline wasteland showed small, numerous oil glands at adaxial side. In population SSR from desert flats, oil glands were present on both adaxial and abaxial leaf surface.

Anatomical modifications in the *S. oleoides* population collected from different environmental conditions were very peculiar. The desert/semi-desert populations showed stem modifications like increased epidermal thickness, collenchymatous thickness, cortical region thickness and cell area, vascular bundle area and xylem region thickness. Leaf modifications like increased midrib thickness, cortical cell area, metaxylem and protoxylem area, phloem area, adaxial stomatal area, and abaxial stomatal density were the specific features. These modifications were critical for increasing water storage capacity, minimizing water loss from the plant surface, and better conduction of solutes and photosynthates.

The populations from salt-affected lands faced twin menace, ion toxicity and physiological drought, which was managed by development of tissues in stem that involved in preventing water loss (epidermal thickness, collenchymatous thickness and sclerenchymatous thickness) and increasing storage capacity (stem radius, cortical region thickness and pith cell area). Precise modifications in leaf were increased lamina thickness, cortical region thickness and cell area, metaxylem and protoxylem area, oil gland area, vascular bundle area, and stomatal area on both leaf surfaces.

5. Conclusion

It is concluded that structural feature regarding xeromorphy (multilayered epidermis, sclerification in vascular tissue, collenchyma, hairiness, succulence) predominantly contributes to the spread of *S. oleoides* in extreme arid areas. Plasticity in many anatomical features (size and nature of vascular tissue, storage parenchyma, arrangement of spongy and palisade mesophyll, size and density of oil glands, stomatal size, shape, and orientation) ensures its survival in a variety of environmental conditions like salt-affected lands, deserts and semideserts, hot and dry mountains, etc.

Author contribution statement

This work is part of Ph.D. thesis of Ummar Iqbal who performed the experiments under supervision of Mansoor Hameed. Mansoor Hameed and Farooq Ahmad designed the experiment and analyzed data.

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