Pak. J. Bot., 57(2): DOI: http://dx.doi.org/10.30848/PJB2025-2(6)

INVASIVE SUCCESS REGULATED BY MICROMORPHOLOGICAL MODIFICATIONS IN WILD SAGE (*LANTANA CAMARA* L.) FROM ECOLOGICALLY DIVERSE HABITATS

HUMA SHAHID, MANSOOR HAMEED* AND FAROOQ AHMAD

Department of Botany, University of Agriculture, Faisalabad 38040, Pakistan
**Corresponding author's e-mail: hameedmansoor@yahoo.com*

Abstract

Invasive species have been declared as one of the utmost important yet subtle hazards to biological diversity. *Lantana camara*, a shrub of Central and South American origin, has a widespread invasiveness across a broad range of climates distributed up to 2000 m elevation. The present studies were performed to examine comparative anatomy of *L. camara* from different habitats including mountains, forest plantations, roadsides, deserts, saltmarshes and riverbanks to find out the ecological significance of anatomical characteristics that are related to invasion success. The studied population was exposed to an explicit set of environmental conditions. Anatomical traits significantly varied in diverse ecological regions, which were population specific. The proportion of parenchymatous tissue in roots, stem and leaves was increased in the desert population, which improved succulence. Moreover, increased metaxylem, phloem area and mesophyll thickness in this population enabling this population for easier translocation of nutrients and photosynthates. In mountainous habitats, increased cross-sectional area, cortical region thickness and epidermal cell area in roots, cortical cell area in stem and phloem area in leaves assisted these populations in minimizing water loss and improving water storage capacity. Sclerenchyma and vascular bundle area were more developed in the roadside populations providing mechanical strength to softer metabolically active tissue. Water availability was limited in the roadside population, hence critically important for survival. A greater number of leaves and greater leaf area were linked to better photosynthesis, which were increased in the riverbank populations where sufficient moisture was available for growth and development. All these ensure invasive success of *L. camara populations* in a variety of habitats either by minimizing water loss from plant body or storing more water in parenchymatous tissue. It was concluded that invasive success of *L. camara* relied on high degree of plasticity in its macro- and micro-morphological traits, which were specific for specific habitats.

Key words: Invasive species; Anatomical modifications; Habitat diversity; Sclerenchyma; Parenchyma; Vascular tissue.

Introduction

Plant invasions are made easier by the combination of three factors: background of commencement (propagule density and dwelling period), inconspicuousness (properties of receipt localities), and intrusiveness (species characteristics) (Foxcroft *et al.,* 2011). Certain intrinsic traits prevent plants from becoming invasive. Weedy plants have a broad ecological amplitude because of their rapid sexual and asexual multiplication, quicker development from seedling to mature stage, increased stress tolerance, and variety. The development of invasive potential is further influenced by life form, plant height, seed size, polyploidy, and ease of hybridization (Moura *et al.*, 2021). The site (where the propagule was introduced), the introduction season, and the geographic area all affect survival and propagation strength (Gioria *et al.*, 2023).

Abiotic stressors typically alter the amount of water available in the surroundings and influence woody plants' ability to transport water. A negative pressure gradient produced by leaf transpiration moves water through the xylem conduit in woody plants (Schenk *et al.*, 2021). Since it controls the ratio of carbon uptake (photosynthesis) to water loss (transpiration), leaf stomatal regulation is essential in situations of abiotic stress (Muhammad *et al.*, 2021). Woody plants modify their anatomical and morphological characteristics as the stress persists. For instance, they lengthen, become denser, and dig deeper roots to absorb water and nutrients more effectively from the soil when the amount of water available in the soil diminishes (Zou *et al.*, 2022). The way that woody plants carry water and react to abiotic stress is also significantly influenced by their leaf shape. For instance, thicker epidermis and cuticles reduce water permeability, which enables plants to adjust to varying water conditions (Seufert *et al.*, 2022). Furthermore, woody plants can modify the quantity, size, and thickness of their leaves to adjust to various moisture, temperature, and nutritional conditions (Peguero-Pina *et al.*, 2020). In response to abiotic stressors, woody plants can also modify the anatomical structure of their xylem to control hydraulic function. To improve the safety of water transmission, for example, they can build conduits that are thinner and have thicker walls (Li *et al.*, 2023).

Lantana camara is a tropical invasive species, which disturbs ecosystems and causes degradation of biodiversity across 60 countries and islands (Kifetew & Woldu, 2021). Its maximum diversity is in north and Central America and in the Caribbean region (Taylor *et al.*, 2012). The present study was focused on the plasticity in structural modifications of *L. camara* that assure its invasive success in a variety of habitats. It is, therefore, hypothesized that invasive success in *L. camara* may be due to anatomical modifications that may be specific for ecologically different habitats, The research questions to be addressed are: 1) Is there any variation in anatomical features of *L. camara* that is naturally growing in different ecological regions? 2) If yes, then how do these modifications contribute to ecological success of this species? and 3) Is there any relationship between soil physicochemical and plant macro- and micro-morphological traits?

Material and Methods

Study sites: Wild sage (*Lantana camara* L.) plants belonging to the Verbenaceae family were naturally found in various regions of Punjab, Pakistan (Fig. 1). A total of twelve populations of this particular species were gathered from six distinct ecological zones, which were selected based on different edaphic, climatic, and topographic conditions (Fig. 2). These zones encompass mountainous areas (Fort Munro, Knotti), forest plantations (Gatwala and Changa Manga), roadside areas (Rasool Headworks and Lahore Islamabad Motorways), deserts (Derawar Fort and Nawab Din Fort), saltmarshes (Kalar Kahar Lake, Sahianwala saltmarsh), and riverbanks (Rasool Jhelum River and Treemu Chenab River).

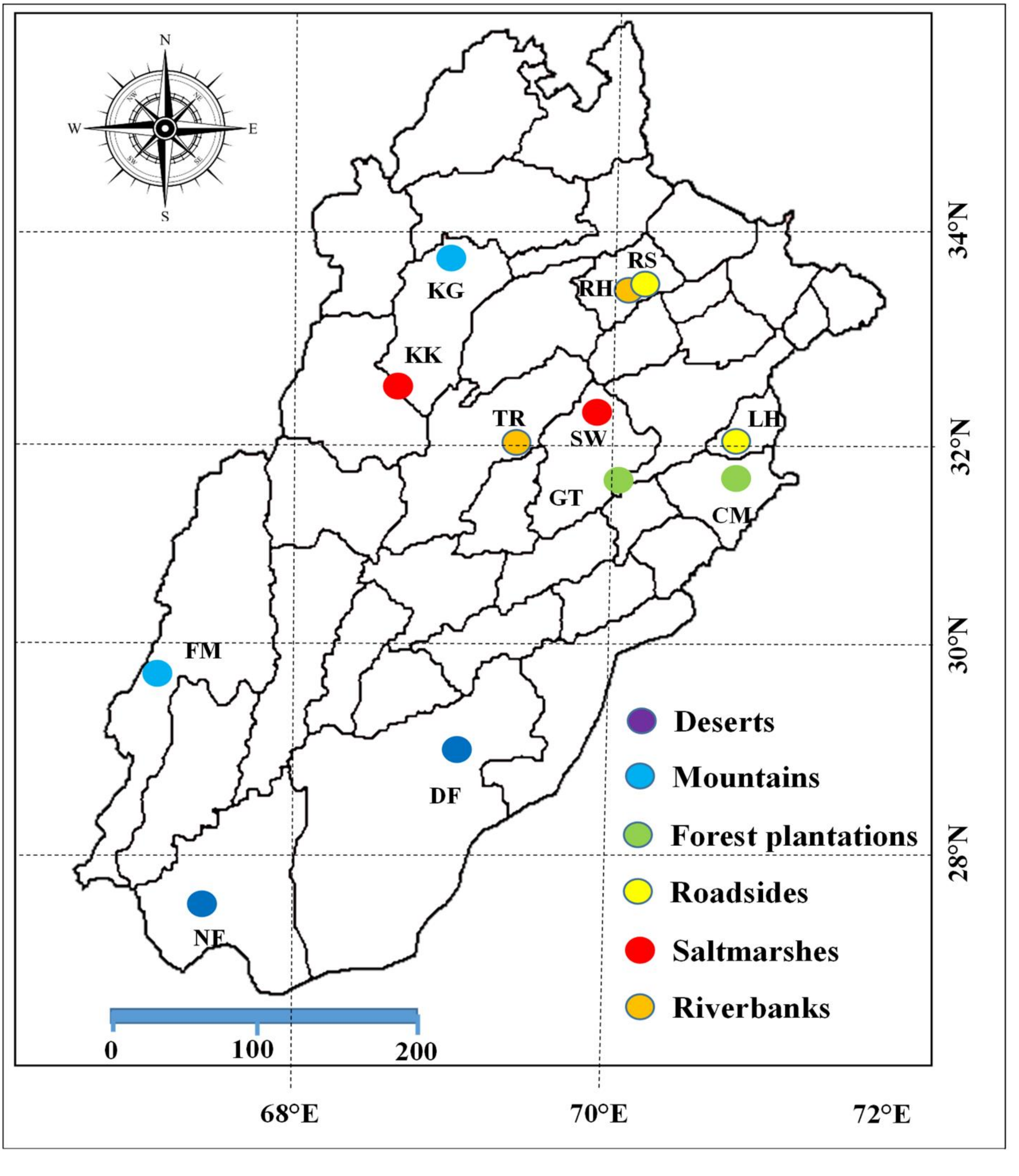

Fig.1. Map of the Punjab showing collection sites of different populations of *lantana camara* L.
DF- Derawar Fort, NF- Nawab Din Fort, FM-Fort Munro, KG- Knotti Garden, GT- Gatwala Plantation, CM-Changa Manga Plantation, RH-Rasool, LH-Lahore-Islamabad Motorways, KK-Kalar Kahar Lake, SW-Sahianwala wetland, RH-Rasool-River Jhelum, TR-Treemu-River Chenab

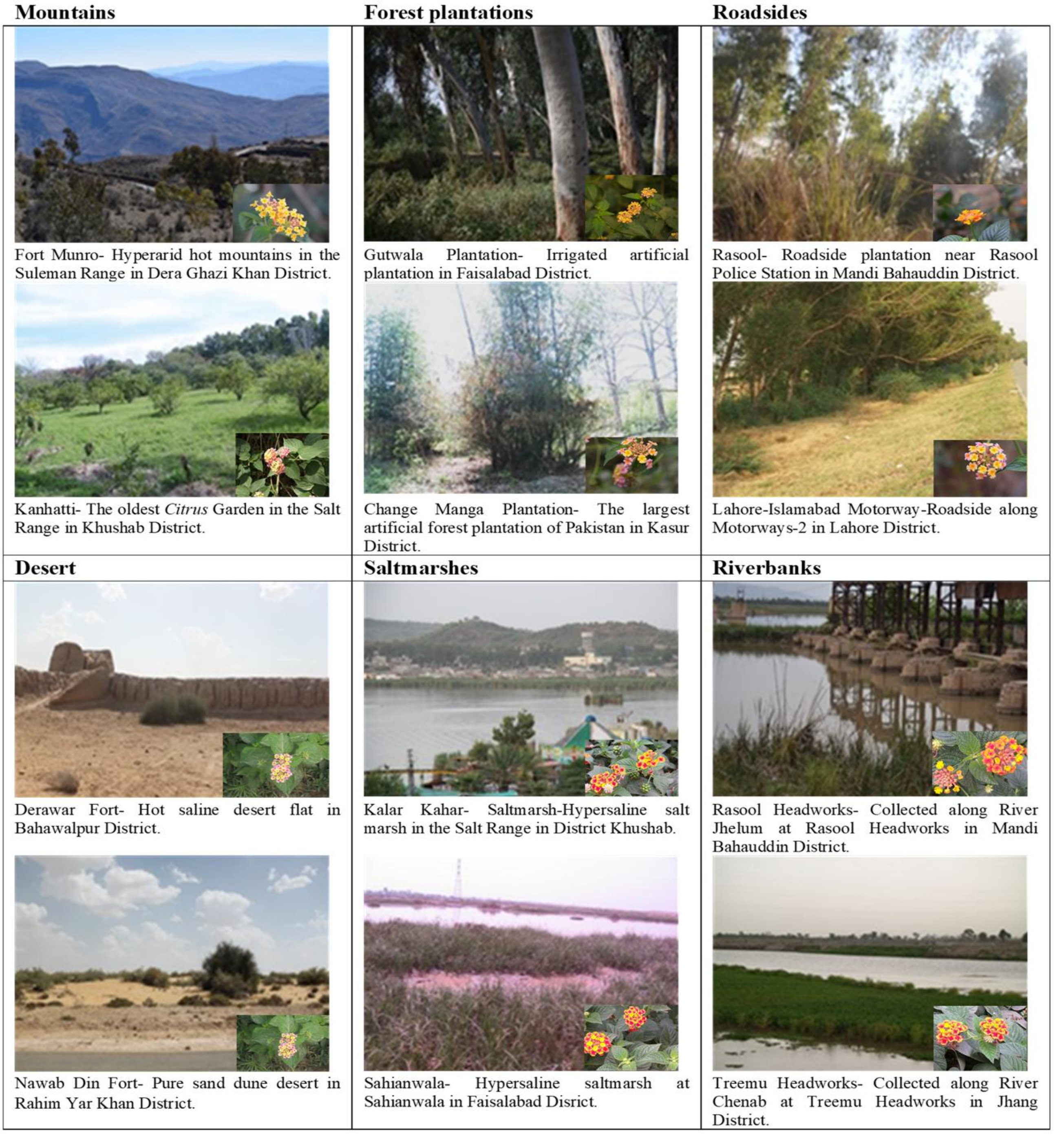

Fig. 2. Pictorial view and habitat description of collection sites of *Lantana camara* L. populations in their natural habitats.

Collection of soil and plants: For the purpose of gathering plant and soil samples, the dominant population from each study location was the focus. Six plants were selected and treated as replications ($n = 6$), three of which were from the marginal area and three from further within the population. The samples were promptly deposited in an icebox for further analysis after being packed in zipper bags. Samples of soil from around each plant were gathered and placed in a plastic zipper bag for physicochemical examination.

Physiographic data: Global Positioning System (Garmin, eTrex Venture HC, Germany) was used to determine the coordinates and altitude like geographic data. Meteorological data was taken from the Meteorological Department of Pakistan Islamabad (https://rmcpunjab.pmd.gov.pk/metData.php).

Soil analysis: To ascertain the physicochemical characteristics, soil was collected at a depth of 15 to 20 cm close to the roots. A 200 g sample of soil was obtained, well mixed, then baked for a week at 70°C to dry it fully. To estimate ECe, saturation percentage, and ionic content, saturation paste was made. A formula determined the percentage of saturated soil:

Saturation percentage = Weight of a saturated paste – Dry weight of soil

Table 1. Environmental traits of *Lantana camara* collected from ecologically different habitats.

Habitats	Elevation (m a.s.I.)	Longitude	Latitude	Annual rainfall (mm)	Maximum temperature (°C)	Minimum temperature (°C)
Mountains						
Fort Munro	1421	29°56'07.79"E	70°02'10.29"N	607	37	-2
Knotti Garden	599	32°41'08.19"E	72°14'56.83"N	410	38	5
Forst plantations						
Gatwala Plantation	194	31°28'22.67"E	73°12'38.91"N	342	45	8
Changa Manga Plantation	204	31°04'50.11"E	73°59'58.03"N	610	44	6
Roadsides						
Rasool	242	32° 42'02 27"E	74° 34'47.49"N	388	46	7
Lahore-Islamabad Motorways	212	31°28'58.78"E	74°14'05.73"N	612	45	6
Deserts						
Derawar Fort	104	28°49'22.92"E	71°20'43.27"N	180	49	16
Nawab Din Fort	103	29°08'19.75"E	71°16'06.36"N	200	51	20
Saltmarshes						
Kalar Kahar Lake	646	32°46'18.34"E	72°42'58.49"N	250	43	3
Sahianwala wetland	189	31°42'09.96"E	73°12'01.12"N	367	47	11
Riverbanks						
Rasool-River Jhelum	216	32°42'02.81"E	73°33'10.93"N	387	42	4
Treemu-River Chenab	152	31°09'43.09"E	72°10'10.58"N	378	46	5

Using the techniques outlined by Richards (1954), the pH and ECe of the soil were determined using a portable pH/Electrical Conductivity Meter (WTW series InoLab pH/Cond 720, USA).

A 3:1 mixture of nitric and perchloric acid was used to digest soil samples in order to estimate the levels of Na^+ and K^+ using a flame-photometer (Model 410, Sherwood Scientific Ltd., Cambridge, UK). An atomic absorption spectrophotometer (Model AAnalyst 3000; Perkin Elmer, Norwalk, CT) was used to record the Ca^{2+}. A chloride meter (Model 926; Sherwood Scientific Ltd., Cambridge, UK) was used to measure the Cl^- in the soil.

Morphological traits: Following the collecting of plant samples (three samples were randomly selected from each population of each species), data was collected. The stem's length was measured from bottom to top. Five leaves from each plant were measured at fixed places to determine the leaf area. The formula used to compute the leaf area was as follows (Schrader *et al*., 2021):

Area = Length x Width x Correction Factor (0.71)

Each leaf's average area was determined by multiplying it by the total number of leaves on each plant.

Anatomical parameters: In accordance with Ruzin (1999), a 2-cm section of the root, stem, and leaves were removed and immediately stored in a formalin-acetic alcohol solution. Each organ was divided into sections with a double-edged razor blade and dried with ethanol grades. The sections were stained with fast green and safranin. A compound microscope (Nikon 104, Japan) equipped with an ocular micrometer was used to measure various tissues and cells.

Statistical analysis

Using CoStat (v. 6.400), the data were subjected to a one-way analysis of variance (ANOVA) with six replications. Data were averaged for each population replication after five plants were chosen at random from each population. Principal component analysis was used to examine the association between plant characteristics and soil using XLSTAT (v. 2014).

Results

Environmental and soil physicochemical traits: Rainfall was the highest (612 mm) at Lahore Islamabad Motorways, ,while maimum and minimum temperatures were the lowest at mountainous hanotat Fort Munro (37 and -2°C respectively) at this site. The minimum annual rainfall (180 mm) was observed from Derawar Fort and maximum temperatures (51 and 20°C) were at Nawab Din Fprt, both from the deserts (Table 1). Among mountains, the lowest pH was at Fort Munro (5.6), whereas soil K^+ (370 mg kg^{-1}) and Ca^{2+} (366 mg kg^{-1}) were the highest (Table 2). Soils from the Gatwala forest plantation had the maximim pH (9.2). Saturation percentage was the lowest (12%) at Nawab Din Fort, while soil K^+ was the minimum (63 mg kg⁻1) at Derawar fort, both from deserts. The saltmarsh population from Sahianwala wetland exhibited the greatest soil ECe (28 dS m^{-1}), Na^+ (5487 mg kg^{-1}) and Cl^- (2378 mg kg^{-1}), while the lowest soil Ca^{2+} (56 mg kg^{-1}). Among riverbank populations, saturation percentage was the highest (32.4%) at Rasool, whereas soil ECe (1.2 dS m^{-1}), Na^+ (59 mg kg^{-1}) and Cl^- (156 mg kg^{-1}) were the lowest at Treemu.

Morphological parameters: The Fort Munro population from mountains showed the maximum root length (18.3 cm), while the minimium leaf area (574.8 cm^2) was recorded at this site (Table 3). The lowest number of leaves (932.0) were observed in the Changa Manga forest plantation and stem length (1.6 m) in the saltmarsh population from Sahianwala. The roadside population from Lahore-Islamabad Motorways possessed the highest number of leaves (1687.3) and the shortest roots (9.0 cm). The Treemu population from riverbank showed the maximum stem length (2.3 m) and leaf area (4978.7 cm^2).

Table 2. Soil physicochemical traits of *Lantana camara* collected from ecologically different habitats.

Habitats	pH	ECe (dS m^{-1})	SP (%)	Na^+ (mg kg^{-1})	Cl^- (mg kg^{-1})	K^+ (mg kg^{-1})	Ca^{2+} (mg kg^{-1})
Mountains							
Fort Munro	5.6	1.6	26.7	76	267	145	145
Knotti Garden	8.1	2.1	27.8	105	346	370	366
Forst plantations							
Gatwala Plantation	9.2	3.2	27.6	309	434	157	145
Changa Manga Plantation	7.3	1.3	29.6	67	278	165	143
Roadsides							
Rasool	8.0	4.0	30	461	456	124	143
Lahore-Islamabad Motorways	7.8	2.8	32	176	308	175	134
Deserts							
Derawar Fort	8.6	8.6	19	1155	1076	63	62
Nawab Din Fort	8.5	1.5	12	77	234	176	35
Saltmarshes							
Kalar Kahar Lake	7.8	17.8	31.8	3056	1769	122	68
Sahianwala wetland	8.3	28.3	32.2	5487	2378	124	56
Riverbanks							
Rasool-River Jhelum	8.3	1.3	32.4	64	268	250	134
Treemu-River Chenab	7.2	1.2	30.8	59	156	272	180

Root anatomy: The population from mountainous habitat (Knotti Garden) showed the maximum root area ((4.8 mm²), epidermal thickness (47.2 µm), cortical thickness (496.0 µm), while the minimum epidermal cell area (841.4 µm²) and cortical cell area (841.4 µm²). The forest plantations Gatwala population represented the lowest epidermal cell area (2103.5 µm²) and epidermal thickness (14.2 µm).The popuations collected from Changa Manga forest plantation and Lahore-Islamabad Motorways depicted the minimum metaxylem area (3786.3 µm²). The minimum cortical thickness (66.1 µm) and maximum vascular bundle area (16617.7 µm²) was observed in the roadside population Rasool (Table 3, Fig. 3). The desert poplation Derawar Fort represented the maximum cortical area (3365.6 µm²), while Nawab Din Fort population showed the maximum metaxylem area (17669.4 µm²). Plants collected from the saltmarsh Sahianwala wetland had the maximum phloem area (2524.2 µm²) and the minimum vascular bundle area (1472.5 µm²). The riverbanh population Rasool showed the largest epidermal cells (2103.5 (µm²).

Stem anatomy: The mountainous population Fort Munro represented the highest cortical area (62053.3 µm²) and the minimum phloem area (631.1 µm²) and hair lengh (14.2 µm). The population from Knotti Garden showed the smallest epidermal cells (841.4 µm²). The Forest plantations Gatwala population showed the minimum vascular region area (0.1 µm²) and metaxylem area (841.4 µm²), while the maximum epidermal thickness (47.2 µm) was observed at Changa Manga forest plantation (Table 3, Fig. 4). The roadside Rasool population had the maximum vascular bundle area (1.7 µm²). The broadest metaxylam vessels (3834.7µm²) and the thickest stems (1209.2 µm) were noted in the Nawab Din Fort population from deserts, while sclerenchyma area was the minimum (22928.2 µm²)at this site. The saltmarsh habitat Kalar Kahar showed the minimum epidermal thickness (18.9 µm) and cortical area (13672.8 µm²), while Sahianwala population showed the maximum phloem area (1682.8 µm²). The riverbank population Rasool represented the maximum epidermal cell area (2103.5 µm²) and sclerenchyma area (51325.5 µm²). The Treemu population showed the minimum pith area (0.5 µm²) but the maximum hair length (85.0 µm).

Leaf anatomy: The Fort Munro population from mountains showed the maximum phloem area (2524.2 µm²) and the minimum mesophyll cell area (1051.8 µm²), while the Knotti Garden population had the thickest lamina (170.0 µm) and midrib (746.3 µm). The smallest epidermal cells (841.4 µm²) were seen in this population (Table 3, Fig. 5). The population from Gatwala forest plantation displayed the thickest epidermis (37.8 µm) and the thinnest lamina (70.9 µm). The Changa Manga forest plantation population showed the minimum parenchyma thickness (132.3 µm) and the maximum lamina thickness (170.0 µm). Among roadsides populations, plants collected from Lahore-Islamabad Motorways revealed the thinnest epidermis (14.2 µm), narrowest metaxylem vessels (841.4 µm²) and the lowest phloem area (631.1 µm²). The Derawar Fort population from deserts showed the broadest metaxylem vessels (2524.2 µm²). The desert population from Nawab Din Fort showed the greatest parenchyma thickness (8414.0 µm²) and mesophyll cell area (5679.5 µm²). The saltmarsh population from Sahianwala wetland displayed the thickest epidermis (37.8 µm) and parenchyma (326.0 µm²), while vascular bundle area was the minumum (0.07 µm²) in this population. Midrib thickness was the maximum (406.2 µm) in riverbank population from Rasool.

Pearson's correlation coefficient among environmental/ soil physicochemical traits and plant morho-anatomical traits ($p<0.05$): Root area and root epidermal thickness were positively correlated with potassium,while a positive correlation was observed between root epidermal thickness and soil Ca^{2+}. Root metaxylem area negatively correlated with saturation percentage. Stem epidermal thickness was negatively correlated with elevation and soil Cl^-. A negative association of stem metaxylem area soil pH, stem cortical area positively associated with elevation (Table 4).

Table 3. Morpho-anatomical traits of *Lantana camara* collected from ecologically different habitats.

Habitats	Mountains		Forest plantations		Roadsides		Deserts		Saltmarshes		Riversides	
Collection sites	**M-Fm**	**M-Kg**	**F-Gt**	**F-Cm**	**Rd-Rs**	**Rd-Lh**	**D-DF**	**D-Nd**	**S-Kk**	**S-Sh**	**Rv-Rs**	**Rv-Th**
Morphology												
Stem length (m)	1.9c	1.8c	1.8c	1.8c	1.7d	1.8c	1.9c	2.1 b	1.8c	1.6e	1.9 c	2.3 a
Leaves per plant	987.2e	1109.1d	985e	932.0e	1043.4d	1687.3a	1145.4c	1043.5d	1123.2d	1209.1c	1098.0d	1372.3b
Leaf area (cm^2)	574.8f	1483.4d	1109.5e	858.9f	1248.3e	2657.8c	1494.9d	901.2e	3234.2b	2135.6c	2213.6c	4978.7a
Root length (ft)	18.3a	9.1d	12.2c	9.1d	15.2b	9.0d	15.8b	12.5c	15.1b	12.3c	15.5b	18.2a
Root anatomy												
Root area (mm^2)	4.6a	4.8a	4.4b	2.8d	2.1e	3.0d	3.3c	3.4c	2.7d	2.2e	4.5a	3.7c
Epidermal cell area (μm^2)	2103.5a	841.4d	2103.5a	1262.1b	1262.1b	1262.1b	1262.1b	1262.1b	1051.8c	1262.1b	2103.5a	1044.9c
Epidermal thickness (µm)	37.8b	47.2a	14.2e	33.1c	33.1c	28.3d	28.3d	33.1c	33.1c	18.9e	33.1c	37.8b
Vascular bundle area (μm^2)	4627.7d	5048.4d	15776.3a	10938.2b	16617.7a	5048.4d	12410.7b	6100.2c	7151.9c	1472.5f	6941.6c	3155.3e
Phloem area (μm^2)	2313.9b	1682.8c	1262.1d	1262.1d	1262.1d	2524.2a	1051.8e	1472.5c	1262.1d	2524.2a	841.4f	841.4f
Metaxylem area (μm^2)	7151.9e	5048.4f	4627.7f	3786.3g	15776.3b	3786.3g	12200.3c	17669.4a	8203.7e	5258.8f	10096.8d	7572.6e
Cortical cell area (μm^2)	2103.5c	841.4f	1262.1d	1262.1d	1472.5e	3365.6a	3365.6a	1262.1d	1051.8e	1996.7c	2103.5c	2734.6b
Cortical thickness (µm)	226.7e	496.0a	439.3b	240.9d	66.1g	198.4f	240.9d	255.1d	410.9b	311.7c	250.3d	255.1d
Stem anatomy												
Epidermal thickness (µm)	23.6e	37.8c	28.3d	47.2a	42.5b	47.2a	33.1d	47.2a	18.9e	37.8c	37.8c	42.5b
Epidermal cell area (μm^2)	1472.5c	841.4e	1262.1c	841.4e	1051.8d	1051.8c	1472.5c	841.4e	1682.8b	1051.8d	2103.5a	1262.1c
Vascular region area (mm^2)	0.6c	0.5c	0.1e	1.4b	1.7a	0.5c	0.3d	0.2e	0.5c	0.1e	0.1e	1.3b
Metaxylem area (μm^2)	3365.6b	1682.8e	841.4f	2734.6c	2679.5c	1472.5e	1051.8f	3834.7a	2313.9d	841.4f	2103.5d	3786.3a
Phloem area (μm^2)	631.1f	1051.8d	841.4e	631.1f	1051.8d	1472.5b	1051.8d	1262.1c	841.4e	1682.8a	1262.1c	631.1f
Sclerenchyma area (μm^2)	28607.6d	41439.0b	41439.0b	38914.8c	29238.7d	35759.5c	26504.1e	22928.2f	24611.0e	27555.9d	51325.5a	19983.3g
Cortical cell area (μm^2)	62053.3a	28397.3c	27976.6c	25242.0d	14724.5e	32814.6b	35128.5b	29869.7c	13672.8f	17038.4e	9255.4g	11569.3f
Stem hair length (µm)	14.2e	33.1d	70.9b	28.3d	33.1d	33.1d	18.9e	47.2c	33.1d	52.0c	70.9b	85.0a
Pith area (mm^2)	2.2a	0.6e	1.8b	1.1d	0.8e	1.5c	0.6e	1.1d	1.6c	1.5c	2.1a	0.5e
Stem radius (µm)	779.4c	722.7c	722.7c	949.4b	836.0b	1161.9a	755.7c	1209.2a	779.4c	637.7d	888.0b	788.8c
Leaf anatomy												
Epidermal thickness (µm)	28.3c	33.1b	37.8a	33.1b	14.2e	14.2e	18.9d	23.6c	18.9d	37.8a	18.9d	33.1b
Epidermal cell area (μm^2)	1472.5c	841.4f	1893.2a	1051.8e	1472.5c	1682.8b	1051.8e	1051.8e	1051.8e	1262.1d	1472.5c	1262.1d
Vascular bundle area (mm^2)	0.11g	0.23e	0.27d	0.39e	0.46a	0.13g	0.20f	0.29d	0.41b	0.07g	0.31c	0.34c
Metaxylem area (μm^2)	1682.8c	1262.1d	1893.2b	1051.8e	1262.1d	841.4f	2524.2a	1262.1d	2103.5b	1262.1d	1682.8c	1262.1d
Phloem area (μm^2)	2524.2a	841.4f	1262.1d	1262.1d	1472.5c	631.1g	1051.8e	631.1g	1893.2b	1051.8e	1682.8c	841.4f
Parenchyma thickness (µm)	240.9d	278.7b	288.1b	132.3f	240.9d	222.0e	269.2c	269.2c	269.2c	326.0a	240.9d	283.4b
Parenchyma cell area (μm^2)	1262.1f	4417.4c	5258.8b	2103.5e	2524.2e	2103.5e	3786.3c	8414.0a	3365.6d	3365.6d	1472.5f	2734.6e
Mesophyll cell area (μm^2)	1051.8f	3786.3b	3365.6c	1051.8f	1682.8e	2313.9d	1472.5e	5679.5a	3576.0b	2313.9d	1051.8f	2103.5d
Lamina thickness (µm)	103.9c	170.0a	70.9f	170.0a	127.5b	127.5b	108.6c	85.0e	85.0e	85.0	75.6f	99.2d
Midrib thickness (µm)	637.7c	746.3a	609.3c	453.4e	694.3b	481.8e	410.9f	552.6d	614.0c	510.1d	406.2f	609.3c

Means sharing similar letter are statistically not significant ($p<0.05$)

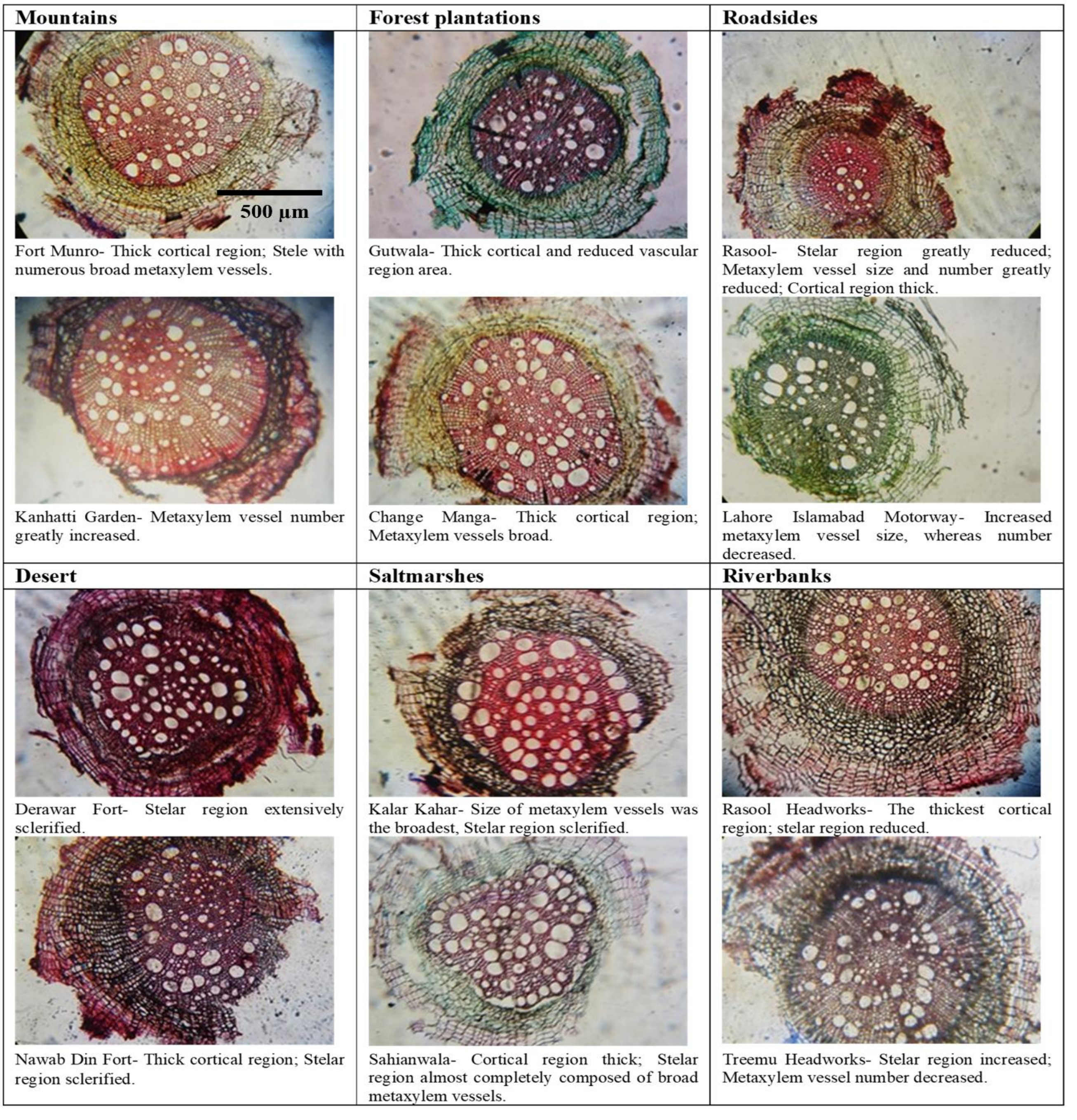

Fig. 3. Root transverse sections of different *Lantana camara* L. populations collected from different ecozones.

Leaf phloem area was positively associated with elevation and negatively correlated with maximum and minimum temperatures. Leaf metaxylem area and cortical thickness negatively correlated with annual rainfall. Leaf cortical area negatively correlated with annual rainfall and saturation percentage, and positively associated with minimum temperature. Lamina thickness was positively correlated with soil Ca^{2+}.

Relationship among environmental/soil physicochemical traits and plant morpho-anatomical traits: The principal component analysis presented six isolated clusters of soil, environmental and plant traits (Fig. 6). Annual rainfall, soil Ca^{2+}, K^+, and root epidermal thickness, stem vascular region area and metaxylem area, and leaf midrib thickness were clustered in a close association in the mountainous habitat Knotti Garden, Changa Manga forest plantation, Treemu riverbank and Lahore-Islamabad Motorways roadside. In the second cluster, minimum and maximum temperatures were connected with root metaxylem area, and leaf parenchymatous cell area and stem length at Rasool roadside. The stem length, leaves per plant, stem epidermal thickness and stem radius, and leaf vascular bundle area were associated with Nawab Din Fort desert. Soil ECe, Na^+ and Cl^-, leaf area, root cortical cell area, stem hair length, phloem area, and leaf epidermal thickness were associated with Derawar Fort desert. Root length, phloem area and cortical thickness, stem epidermal cell area, leaf parenchymatous thickness and metaxylem area were associated with Gatwala forest plantation, and saltmarsh habitats at Kalar Kahar and Sahianwala. The last cluster displayed a clustering among elevation, saturation percentage, root area, stem sclerenchyma area, cortical area, pith area, and leaf phloem area at Fort Munro mountainous region and Rasool riverbank.

Fig. 4. Stem transverse sections of different *Lantana camara* L. populations collected from different ecozones.

Discussion

Anatomical traits are of great ecological and taxonomic significance, however high degrees of variation were reported in various plants (Makbul *et al.,* 2011). Parenchyma vascular and sclerenchyma tissue are critical for the survival of a species that is linked to abiotic stress tolerance (Tester & Bacic, 2005). Water storage conservation in plants is either by prevention of water loss from surface via thickening of epidermis (Mauseth, 2004) or by increasing storage capacity in parenchymatous tissue (De Micco & Aronne, 2012). Water conduction through metaxylem vessels contributes to water storage (Vasellati *et al.*, 2001). Sclerification provides mechanical support to delicate tissues (Vendramini *et al.,* 2002) by preventing tissues from collapse when water availability is limited (Moulia *et al.,* 2006). Trichome length and density, especially on leaf surface, control transpiration rate via lowering leaf temperature (Pérez-Estrada *et al.*, 2000; Zhao *et al.*, 2010), blocking wind speed (Benz & Martin, 2006), and by preventing the leaf surface from direct exposure of radiation (Wagner *et al.*, 2004).

Table 4. Pearson's correlation coefficient among environmental/soil physicochemical traits and plant morho-anatomical traits.

Variables	Ele	ARF	MxT	MnT	pH	EC	SP	Na	Cl	K	Ca
MSL	-0.087	-0.170	0.192	0.124	-0.205	-0.516	-0.384	-0.505	-0.297	0.329	0.010
MNL	-0.251	0.181	0.168	-0.021	0.000	0.079	0.295	0.069	-0.023	0.129	0.012
MLA	-0.236	-0.162	0.113	-0.196	-0.042	0.186	0.446	0.187	0.284	0.264	0.024
MRL	0.344	-0.260	-0.064	-0.258	-0.403	0.004	0.007	0.002	0.143	-0.214	-0.250
RRA	0.397	0.104	-0.572	-0.306	-0.122	-0.556	-0.129	-0.549	-0.398	**0.595**	0.550
REC	0.283	0.211	-0.260	-0.273	-0.091	-0.244	0.051	-0.229	-0.283	-0.187	-0.180
RET	0.413	0.188	-0.495	-0.333	-0.518	-0.444	-0.052	-0.442	-0.136	**0.606**	**0.586**
RVB	-0.256	-0.194	0.211	0.156	0.390	-0.273	-0.140	-0.307	-0.057	-0.394	-0.069
RPH	0.383	0.497	-0.211	-0.124	-0.300	0.351	0.132	0.363	-0.023	-0.134	-0.026
RMX	-0.202	-0.568	0.505	0.541	0.205	-0.133	**-0.628**	-0.144	-0.024	-0.256	-0.404
RCC	-0.185	0.091	0.262	0.092	-0.121	-0.024	0.028	-0.041	-0.202	-0.255	-0.261
RCT	0.144	-0.260	-0.322	-0.082	0.296	0.215	0.042	0.207	0.342	0.407	0.379
SET	**-0.626**	0.258	0.437	0.410	0.160	-0.335	-0.134	-0.304	**-0.628**	0.269	0.083
SEC	0.207	-0.231	-0.240	-0.359	-0.055	0.072	0.270	0.056	0.333	-0.129	-0.235
SVR	-0.008	0.352	-0.046	-0.291	-0.427	-0.314	0.258	-0.307	-0.183	0.039	0.243
SMX	0.251	0.156	-0.030	-0.123	**-0.580**	-0.466	-0.258	-0.439	-0.215	0.202	-0.020
SPH	-0.404	-0.163	0.365	0.452	0.493	0.466	-0.009	0.472	0.022	-0.079	-0.266
SSC	-0.054	0.334	-0.447	-0.299	0.246	-0.323	0.346	-0.313	-0.320	0.393	0.436
SCC	**0.648**	0.385	-0.335	-0.114	-0.495	-0.267	-0.396	-0.279	-0.268	-0.199	0.049
STL	-0.482	-0.231	0.234	0.052	0.367	-0.060	0.223	-0.023	-0.198	0.397	0.032
SPA	0.448	0.393	-0.426	-0.487	-0.238	0.074	0.347	0.098	0.089	-0.079	-0.185
SSA	-0.270	0.206	0.371	0.360	0.035	-0.421	-0.404	-0.417	-0.297	0.004	-0.266
LET	0.058	0.108	-0.160	-0.053	-0.018	0.155	0.074	0.197	-0.183	0.292	0.283
LEC	-0.014	0.310	-0.028	-0.262	0.063	-0.173	0.327	-0.168	-0.281	-0.213	-0.132
LVB	-0.258	-0.225	0.131	-0.055	0.127	-0.281	0.070	-0.289	0.177	0.059	0.037
LMX	0.151	**-0.636**	0.031	0.096	0.211	0.213	-0.248	0.166	0.488	-0.428	-0.301
LPH	**0.757**	0.199	**-0.598**	**-0.656**	-0.556	0.053	0.276	0.051	0.295	-0.275	-0.092
LCT	-0.042	**-0.626**	0.180	0.258	0.370	0.507	-0.106	0.504	0.259	0.050	-0.069
LCA	-0.343	**-0.596**	0.537	**0.764**	0.576	0.010	**-0.759**	0.005	0.010	0.024	-0.180
LMS	-0.161	-0.468	0.306	0.497	0.441	0.063	-0.516	0.058	0.189	0.204	-0.033
LLM	0.081	0.502	-0.321	-0.178	-0.269	-0.318	0.104	-0.321	-0.279	0.334	**0.618**
LMD	0.453	0.017	-0.412	-0.328	-0.203	-0.105	0.073	-0.105	0.040	0.371	0.566

Positively significant at $p<0.05$ | Negatively significant at $p<0.05$

Environment: Ele-Elevation, ARF-Annual rain fall, MxT-Maximum temperature, MnT- minimum temperature.
Soil: pH, EC- Electrical conductivity, SP-Saturation percentage, Na- Sodium ion, Cl- Chloride ion, K-potassium ion, Ca- Calcium ion,
Morphology: MSL- Stem length (m), MNL- Leaves per plant, MLA- Leaf area (cm^2), MRA- Root length (m).
Root anatomy: RRA- Root area (mm^2), RCE- Epidermal cell area (µm^2), RET- Epidermal thickness (µm), RVB- Vascular bundle area (µm^2), RPH-Phloem area (µm^2), RMX- Metaxylem area (µm^2), RCC- Cortical cell area (µm^2), RCT- Cortical thickness (µm).
Stem anatomy: SET-Epidermal thickness (µm), fffSEC- Epidermal cell area (µm^2), SVR- Vascular region area (mm^2), SMX- Metaxylem area (µm^2), SPH- Phloem area (µm^2), SSC- Sclerenchyma area (µm^2), SCC- Cortical cell area (µm^2), STL- Hair length (µm), SPA- Pith area (mm^2), SSA-Stem radius (µm).
Leaf anatomy: LET- Epidermal thickness (µm), LEC- Epidermal cell area (µm^2), LVB- Vascular bundle area (mm^2), LMX- Metaxylem area (µm^2), LPH- Phloem area (µm^2), LCT- Parenchyma thickness (µm), LCA- Parenchyma cell area (µm^2),LMX- Mesophyll area (µm^2), LLM-Lamina thickness (µm), LMD- Midrib thickness (µm).

In different environmental conditions, leaf area remains a unique feature of plants that represent their overall growth and impact of environmental conditions (Monteverdi *et al.,* 2008). The riverbank Treemu population in our study represts maximum leaf area. Roots and stems are vital organs of plants for their anchorage and maximum nutrient uptake (Carvalho & Foulkes, 2018).

Different habitats in the diverse regions had different root areas. A decrease in root area was observed at roadsides Rasool population in our studies, and this was due to less quantity of storage and vascular tissues (Boughalleb *et al.,* 2009). Narrow xylem vessels are less subjected to embolism and collapse in response to osmotic stress (Hameed *et al.,* 2009). Increased vascular bundle size was observed at roadsides Rasool population, which is crucial for translocation of water and photosynthates. (Zhang *et al.,* 2009) reported a direct correlation between vessel size and rate of water conduction. Epidermis thickness and cell area were the greatest in population from the mountainous habitat Fort Munro. Epidermis is a first line of defense in plants that is a barrier against the influx of toxic species (Yuan *et al.,* 2016). Thicker epidermis with larger cells can minimize loss of water from plant surface and aid in conservation of water (Parida *et al.,* 2016). Plants that can withstand severe environmental conditions have thick epidermis with coating of waxy layer (Gorb *et al.*, 2022)

According to Hacke *et al.*, (2017), narrow conducting vessels are likely to less prone to collapse under water scarce conditions and narrow phloem vessels were observed at riverbank populations. The plants collected from forest plantation represent some noticeable features like reduced metaxylem vessels size in Changa Manga population.

Reduced metaxylem area is an important step towards better survival to overcome the danger of embolism under restricted supply of water (Vasellati *et al.*, 2001). Increased metaxylem area can be attributed to water and mineral transport (Singh *et al.*, 2013). Root cross-sectional area is mainly due to storage parenchyma that increases the water storage capacity (Nawazish *et al.*, 2006).

Additional cortical thickening in root region is a prominent feature of plants surviving in diverse conditions, which represents their additional ability of more water storage for better growth (Grigore & Toma, 2007). A similar response was found in the population collected from the mountains (Knotti Garden).

Thick epidermis acts as an adaptive strategy of plants under stress conditions (Ristic & Jenks, 2002) and as mechanism for prevention of water loss from leaf surface when water supply is limited (YuJing *et al.*, 2000). Thick epidermis was observed in the population collected from Changa Manga forest plantation. Epidermal cell area increased in population collected from Rasool riverbank. Thick epidermis can limit water loss through plant surface (Nawazish *et al.*, 2006). Large vascular bundles were recorded in Rasool roadside population. The Sahianwala saltmarsh population had smaller vascular bundles, which are responsible for better water uptake as reported by YuJing *et al.*, (2000).

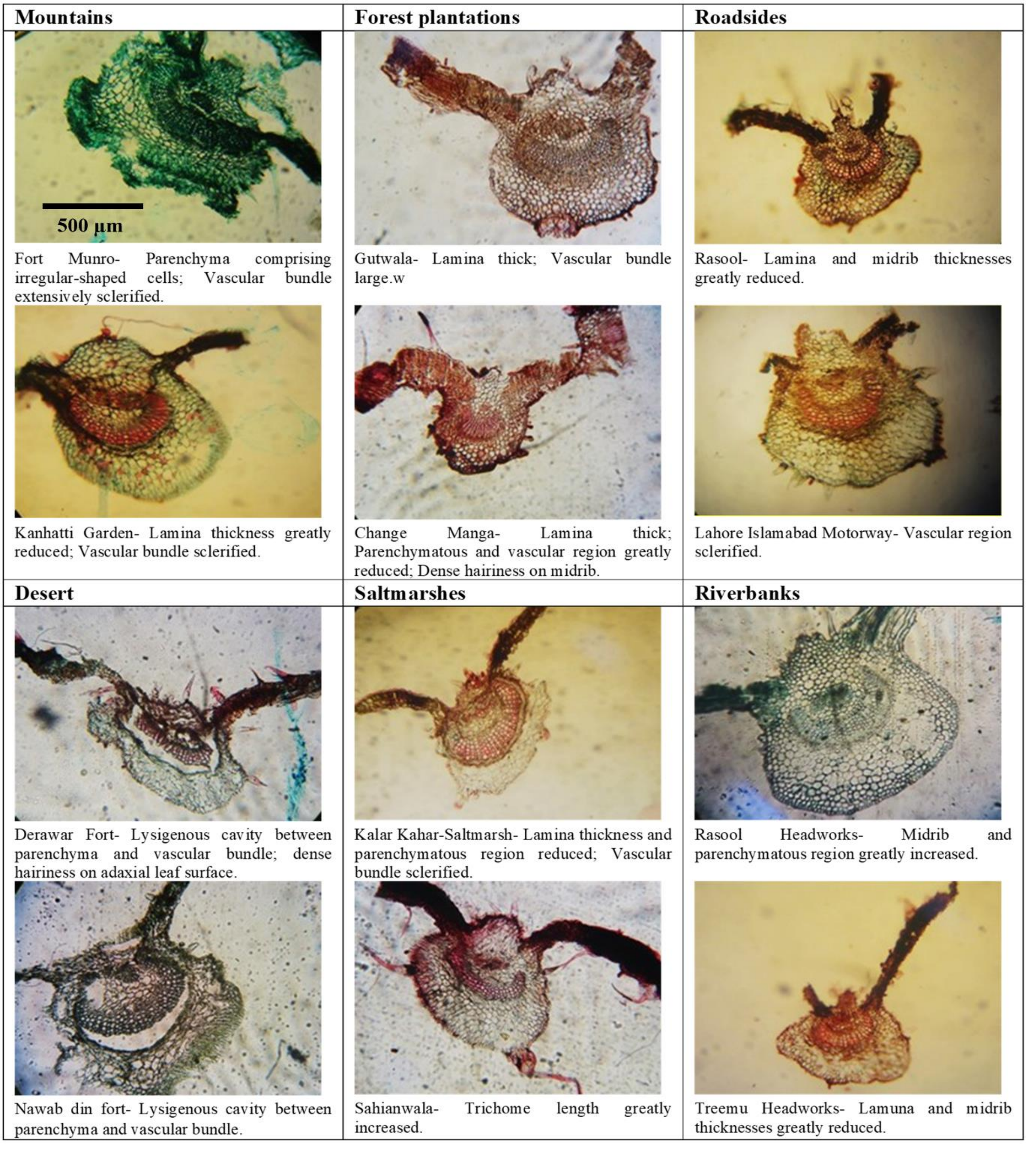

Fig. 5. Stem transverse sections of different *Lantana camara* L. populations collected from different ecozones.

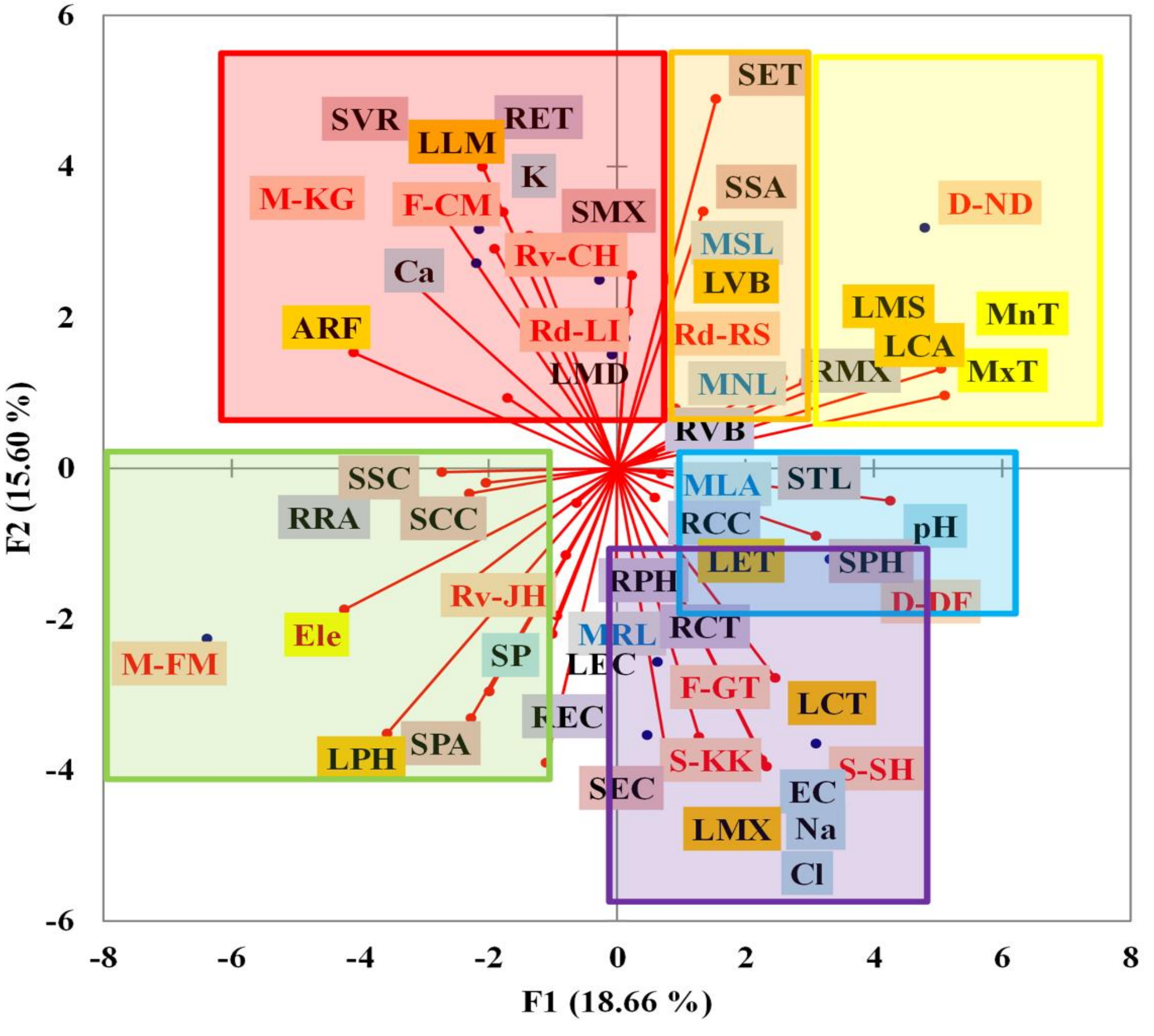

Fig. 6. Relationship among environmental and soil physicochemical traits and plant morpho-anatomical traits.
Ele-Elevation, ARF-Annual rain fall, MxT-Maximum temperature, MnT-Minimum temperature, pH, EC-Electrical conductivity, SP-Saturation percentage, Na-Sodium ion, Cl- Chloride ion, K-potassium ion, Ca- Calcium ion, MSL-Morphology Stem length (m), MNL-Morphology leaves per plant, MLA-Morphology leaf area (µm2), MRA-Morphology root length (ft) RRA- Root area (mm²), RCE-Root epidermal cell area (µm²), RET-Root epidermal thickness (µm), RVB-Root vascular bundle area (µm²), RPH-Root phloem area (µm²), RMX- Root metaxylem area (µm²), RCC- Root cortical area (µm²), RCT- Root cortical thickness (µm), SET-Stem epidermal thickness (µm), SEC-stem epidermal cell area (µm²), SVR-Stem vascular region area (mm²), SMX-Stem metaxylem area (µm²), SPH-Stem phloem area (µm²), SSC-Stem sclerenchyma area (µm²), SCC-Stem cortical area (µm²), STL-Stem hair length (µm), SPA- Stem pith area (mm²), SSA-Stem radius (µm), LET- Leaf epidermal thickness (µm), LEC- Leaf epidermal cell area (µm²), LVB-Leaf vascular bundle area (mm²), LMX-Leaf metaxylem area (µm²), LPH-Leaf phloem area (µm²), LCT-Leaf cortical thickness (µm), LCA- Leaf cortical area (µm²), LMX-Leaf mesophyll area (µm²), LLM-Leaf lamina thickness (µm), LMD-Leaf midrib thickness (µm).

Vascular bundles are the conducting tissues (Parida *et al.*, 2016), that is why transportation of solutes is affected by decline in number of vascular bundles (Sharma *et al.*, 2019). Plants can decrease the size and number of vascular tissues in stressed environmental conditions to survive in severe climatic conditions (Aroca *et al.*, 2012).

In the present studies, metaxylem area decreased at Sahianwala saltmarsh and Gatwala forest plantation. Broad metaxylem vessels are helpful in efficient translocation of nutrients (Smith *et al.*, 2013). Maintenance of turgor potential and sufficient water conduction is ensured by the size of metaxylem. Populations that have efficient structural modifications can survive better in harsh climatic conditions (Hameed *et al.*, 2012). An increase in area of phloem was observed in the Sahianwala saltmarsh population, while it decreased in the least tolerant mountainous population from Fort Munro. Better transportation of photoassimilation is facilitated by larger phloem region and ultimately enhance survival rate of a plant (Ola *et al.*, 2012; Lemoine *et al.*, 2013; Ahmad & Amanullah 2016).

Mechanical strength to plant organs is provided by sclerification and in turn provides resistance from collapsing of soft tissues (Nawaz *et al.*, 2013). In addition, it prevents excessive loss of water. In water scarce environments, sclerification is important for plant survival as confirmed by the studies of Cholewa & Griffith (2004) and Hameed *et al.*, (2012). It is an adaptive strategy to live in harsh climate having greater sclerification around water conducting tissues (Endo *et al.*, 2008). The Treemu riverbank population showed a decrease in sclerenchyma area, while Rasool riverbank population represented an increase in this parameter.

An increase in cortical thickness and cell area was observed in Fort Munro mountains population. To cope with water scarce environments, cortical cell thickness plays vital role in water conservation as they have water storage function (Bell & O'Leary, 2003). A decrease in cortical area was observed in Rasool riverbank population. This is likely due to a decline in development and division of cells as observed in *Juncus* sp. by Al Hassan *et al.*, (2015). Increased proportion of pith was found in stem of population collected from Fort Munro mountains, which is associated with increase in storage capacities of plants under harsh environment (Mitchell *et al.*, 2000).

In our study, a decrease in stem radius was observed in the Sahianwala saltmarsh population indicating low tolerance to salinity stress. The stem area mainly relies on the quantity of parenchymatous region (Fatima *et al.*, 2023). Succulence (increase in storage parenchyma) is among the most common adaptive features in salt tolerant/halophytic species to withstand physiological drought (Parida *et al.*, 2016).

Identification of different plant species and their ability to cope with stresses is determined based on their anatomical features (Naskar & Palit 2015). Anatomical variation is observed in leaf traits of the same species under different environments (Alvarez *et al.*, 2008). In our study, thick epidermis and cuticle layer was observed in the Sahianwala saltmarsh population, which is linked to better ability of this population to tolerate environmental adversaries (YuJing *et al.*, 2000).

Vascular bundle area is concerned with efficient transport of water and nutrients from the soil, and it might be of greater significance under low availability of moisture (Fatima *et al.*, 2023). An increase in vascular bundles was reported by Iqbal *et al*., (2021) in *Salvadora oleoides*, which is associated with our study where an increase in vascular bundles was observed in the Rasool roadside population.

Leaf (midrib and lamina) thickness decreased in the Rasool riverbank population, which support to its better survival under stressed climatic conditions. Similar findings were reported by Hameed *et al*., (2012) in *Panicum antidotale*, while in contradiction Hameed *et al*., (2009) in *Imperata cylindrica* reported an increase in leaf thickness.

Enhancement in parenchymatous areas is related to better storage capacity of plants and an adaptation of plants in harsh climate (Shah *et al.*, 2023). An increase in cortical area in the Nawab Din Fort desert population is responsible for wide distribution of this species as observed by Mondal *et al.*, (2023) in plants. An increase in metaxylem area was observed in the Derawar Fort desert population, while in all other populations this trait was relatively reduced. Better nutrient and water translocation is performed by larger metaxylem vessels (Fatima *et al.*, 2023). Hydraulic conductivity of plants depends on the vessel area (Smith *et al.*, 2013). An increase was reported in the Fort Munro mountainous population in our study. Increased phloem area was previously reported by Ola *et al.*, (2012) in *Leptochloa fusca* and Ahmad & Amanullah (2016) in *Gazania harlequin* Survival rate of plants is increased with increase translocation of photoassimilates, which depends on increased phloem vessels (Lemoine *et al.*, 2013).

Mesophyll thickness and parenchymatous thickness are helpful in increased photosynthesis, which increased in the Derawar Fort desert and Sahianwala saltmarsh populations. This is confirmed by studies of Flowers & Colmer (2008). A decrease in phloem area was observed in the Lahore-Islamabad Motorways population, which is contradictory to the findings of Van Bel & Hafke (2005), who related steepness of the hydraulic gradient with sieve tube elements in phloem. Based on this, the saltmarsh populations can be concluded as the better adapted, where both phloem and sieve area considerably increased.

Conclusion

There was a high degree of variation in anatomical features of *L. camara* natural populations from different ecological regions. The alterations in anatomical features reflected a specific set of environmental conditions to which the natural populations were exposed. High degree of plasticity in macro- and micro-morphological feature was observed in *L. camara* populations collected from different ecological regions, which enable this species to adapt to environmental heterogeneity. The proportion of parenchymatous tissue increased in the desert population which is an indication of increased succulence and storage of higher amount of water, which is responsible for its better success in desert habitats. In mountainous habitats, highest root area, root cortical and epidermal cell area, stem cortical area and leaf phloem area are responsible for better anchorage and enhanced storage capacity in these habitats. Sclerenchyma and vascular bundle area are more developed in the roadside populations, which are involved in prevention of water loss and better conduction of water and nutrients. Lamina and midrib thicknesses increased in the mountainous populations, which represented its better growth in these areas. A greater number of leaves and greater leaf area are linked to better photosynthesis, which were increased in the riverbank populations. Metaxylem, phloem area and mesophyll thickness cause more translocation of nutrients and photosynthates, which increased in the desert populations. In the riverbank populations, phloem and pith area were enhanced that guarantee better conduction of photosynthesis product and better storage of water. Leaf hair length significantly increased in the mountainous populations, which protects these populations from irradiance, high wind velocity and cool temperature. All these ensure invasive success of *L. camara* populations in a variety of habitats.

Acknowledgements

The paper was extracted from the Ph.D. thesis of the first author, which was submitted to the Botany Department, University of Agriculture Faisalabad.

References

Ahmad, I. and S. Amanullah. 2016. Effectiveness of various salinity on leaf growth of *Gazania*. *Int. J. Agron.*, 9: 1-9.

Al Hassan, M., G. Gohari, M. Boscaiu, O. Vicente and M Grigore. 2015. Anatomical modifications in two *Juncus* species under salt stress conditions. *Not. Bot. Horti. Agrobot. Cluj-Napoca*, 43: 501-506.

Alvarez, J.M., J.F. Rocha, S.R. Machado. 2008. Bulliform cells in *Loudetiopsis chrysothrix* (Nees) Conert and *Tristachya leiostachya* Nees (Poaceae): Structure in relation to function. *Braz. Arch. Biol. Technol.*, 51: 113-119.

Aroca, R., R. Porcel and J.M. Ruiz-Lozano. 2012. Regulation of root water uptake under abiotic stress conditions. *J. Exp. Bot.*, 63: 43-57.

Bell, H.L. and J.W. O'Leary. 2003. Effects of salinity on growth and cation accumulation of *Sporobolus virginicus* (Poaceae*). Am. J. Bot.*, 90: 1416-1424.

Benz, B.W. and C.E. Martin. 2006. Foliar trichomes, boundary layers, and gas exchange in 12 species of epiphytic *Tillandsia* (Bromeliaceae). *J. Plant Physiol.*, 163: 648-656.

Boughalleb, N., L. Trabelsi, S/ Harzallah and Fethia. 2009. Antifungal activity from polar and non-polar extracts of some Chenopodiaceae wild species growing in Tunisia. *Nat. Prod. Res.*, 23: 988-997.

Carvalho, P. and M.J. Foulkes. 2018. Roots and Uptake of Water and Nutrients. In: (Ed.): Meyers, R. *Encyclopedia of Sustainability Science and Technology*. Springer, New York, NY.

Cholewa, E. and M. Griffith. 2004. The unusual vascular structure of the corm of *Eriophorum vaginatum*: Implications for efficient retranslocation of nutrients. *J. Exp. Bot*., 55: 731-741.

De Micco, V. and G. Aronne. 2012. Morpho-Anatomical Traits for Plant Adaptation to Drought. In: (Ed.): Aroca, R. *Plant Responses to Drought Stress*. Springer, Berlin, Heidelberg.

Endo, A.1., Y. Sawada, H. Takahashi, M. Okamoto, K. Ikegami, H. Koiwai, M. Seo, T. Toyomasu, W. Mitsuhashi, K. Shinozaki, M. Nakazono, Y. Kamiya, T. Koshiba and E. Nambara. 2008. Drought induction of *Arabidopsis* 9-cis-epoxycarotenoid dioxygenase occurs in vascular parenchyma cells. *Plant Physiol.*, 147: 1984-1993.

Fatima, S., M. Hameed, F. Ahmad, M.S.A. Ahmad, M. Anwar, M. Munir, M. Ashraf, S.M.R. Shah, S. Basharat, I. Ahmad and S. Khalil. 2023. Dramatic changes in anatomical traits of a C_4 grass *Chrysopogon serrulatus* Trin. (Poaceae) over a 1000 m elevational gradient. *J. Mount. Sci*., 20(5): 1316-1335.

Flowers, T.J. and T.J. Colmer. 2008. Salinity tolerance in halophytes. *New Phytol.*, 179: 945-963.

Foxcroft, L.C., S.T.A. Pickett and M.L. Cadenasso. 2011. Expanding the conceptual framework of plant invasion ecology. *Persp. Plant Ecol. Evol. Syst.*, 13: 89-100.

Gioria, M., P.E. Hulme, D.M. Richardson and P. Pyšek. 2023. Why are invasive plants successful? *Annu. Rev. Plant Biol.*, 74: 635-670.

Gorb, E.V., I.A. Kozeretska and S.N. Gorb. 2022. Hierachical epicuticular wax coverage on leaves of *Deschampsia antarctica* as a possible adaptation to severe environmental conditions. *Beilstein J. Nanotechnol.*, 13(1): 807-816.

Grigore, M.N. and C. Toma. 2007. Histo-anatomical strategies of Chenopodiaceae halophytes: Adaptive, ecological and evolutionary implications. *Trans. Biol. Biomed.*, 4: 204-218.

Hacke, U.G., R. Spicer, S.G. Schreiber and L. Plavcová. 2017. An ecophysiological and developmental perspective on variation in vessel diameter. *Plant Cell Environ.*, 40: 831-845.

Hameed, M., M. Ashraf and N. Naz. 2009. Anatomical adaptations to salinity in cogon grass [*Imperata cylindrica* (L.) Raeuschel] from the Salt Range, Pakistan. *Plant Soil*, 322: 229-238.

Hameed, M., T. Nawaz, M. Ashraf, A. Tufail, H. Kanwal, M.S.A. Ahmad and I. Ahmad. 2012. Leaf anatomical adaptations of some halophytic and xerophytic sedges of the Punjab. *Pak. J. Bot.*, 44: 159-164.

Iqbal, U., M. Hameed and F. Ahmad. 2021. Water conservation strategies through anatomical traits in an endangered arid zone species *Salvadora oleoides* Decne. *Turk. J. Bot.*, 45: 140-157.

Kifetew, M. and Z. Woldu. 2021. Impact assessment on an invasive species, *Lantana camara* on indigenous species composition and socio-economic environment around Adama and Bishofitu areas, Ethiopia. *J. Environ. Earth Sci.,* 11(3): 29-42.

Lemoine, R., S. La Camera, R. Atanassova, F. Dédaldéchamp, T. Allario, N. Pourtau, J.L. Bonnemain, M. Laloi, P. Coutos-Thévenot, L. Maurousset, M. Faucher, C. Girousse, P. Lemonnier, J. Parrilla and M. Durand. 2013. Source-to-sink transport of sugar and regulation by environmental factors. *Front. Plant. Sci.*, 4: 1-21.

Li, S., S.Lu, J.Wang, Z.Chen, Y.Zhang, J.Duan, P.Liu, X.Wang and J. Guo. 2023. Responses of physiological, morphological and anatomical traits to abiotic stress in woody plants. *Forests*, 14(9): 1784.

Makbul, S., G.S. Neslihan, N. Durmus and S. Güven. 2011. Changes in anatomical and physiological parameters of soybean under drought stress. *Turk. J. Bot.*, 35(4): 369-377.

Mauseth, J.D. 2004. The structure of photosynthetic succulent stems in plants other than cacti. *Int. J. Plant Sci.*, 165: 1-9.

Mitchell, J.P., C. Summers, T.S. Prather, J. Stapleton and L.M. Roche. 2000. 293 Potential allelopathy of Sorghum-Sudan mulch. *HortScience*, 35: 442B-442.

Mondal, K., S. Raj, K. Thakur, A. Verma, N. Kharwal, A. Chowdhury, S. Sadhu, M. Ram, P. Bishnoi, S. Dutta and A.G. Jain. 2023. Molecular Basis of Plant Adaptation against Aridity. In: (Eds.): Oliveira, M. and A. Fernandes-Silva. *Abiotic Stress in Plants-Adaptations to Climate Change*. IntechOpen, UK.

Monteverdi, C.M., M. Lauteri and R. Valentini. 2008. Biodiversity of plant species and adaptation to drought and salt conditions. Selection of species for sustainable reforestation activity to combat desertification. In: (Eds.): Abdelly, C., M. Öztürk, M. Ashraf and C. Grignon. *Biosaline Agriculture and High Salinity Tolerance*. Birkhäuser Verlag AG, Basel Boston, Berlin.

Moulia, B., C. Coutand and C. Lenne. 2006. Posture control and skeletal mechanical acclimation in terrestrial plants: implications for mechanical modeling of plant architecture. *Am. J. Bot.*, 93: 1477-1489.

Moura, R.F., D. Queiroga, E. Vilela and A.P. Moraes. 2021. Polyploidy and high environmental tolerance increase the invasive success of plants. *J. Plant Res.*, 134(1): 105-114.

Muhammad, I., A. Shalmani, M. Ali, Q.H. Yang, H. Ahmad and F.B. Li. 2021. Mechanisms regulating the dynamics of photosynthesis under abiotic stresses. *Front. Plant Sci.*, 11: 615942.

Naskar, S. and P.K. Palit. 2015. Anatomical and physiological adaptations of mangroves. *Wetlands Ecol. Manage.*, 23: 357-370.

Nawaz, T., M. Hameed, M. Ashraf, S. Batool and N. Naz. 2013. Modifications in root and stem anatomy for water conservation in some diverse blue panic (*Panicum antidotale* Retz.) ecotypes under drought stress. *Arid Land Res. Manage.*, 27: 286-297.

Nawazish, S., M. Hameed and S. Naurin. 2006. Leaf anatomical adaptations of *Cenchrus ciliaris* L. from the Salt Range, Pakistan against drought stress. *Pak. J. Bot.*, 38: 1723-1730.

Ola, H.A.E., E.F. Reham, S.S. Eisa and S.A. Habib. 2012. Morpho-anatomical changes in salt stressed kallar grass (*Leptochloa fusca* L. Kunth). *Res. J. Agric. Biol. Sci*., 8: 158-166.

Parida, A.K., S.K. Veerabathini, A. Kumari and P.K. Agarwal. 2016. Physiological, anatomical and metabolic implications of salt tolerance in the halophyte *Salvadora persica* under hydroponic culture condition. *Front. Plant Sci.*, 7: 1-18.

Peguero-Pina, J.J., A. Vilagrosa, D. Alonso-Forn, J.P. Ferrio, D. Sancho-Knapik and E. Gil-Pelegrín. 2020. Living in drylands: Functional adaptations of trees and shrubs to cope with high temperatures and water scarcity. *Forests*, 11(10): 1028.

Pérez-Estrada, L.B., Z. Cano-Santana and K. Oyama. 2000. Variation in leaf trichomes of *Wigandia urens*: Environmental factors and physiological consequences. *Tree Physiol.*, 20: 629-632.

Richards, L.A. 1954. USDA Laboratory Staff, United State Department of Agriculture, Agriculture Handbook No. 60. U. S. Government Printing Office Washington 25, D. C.

Ristic, Z. and M.A. Jenks. 2002. Leaf cuticle and water loss in maize lines differing in dehydration avoidance. *J. Plant Physiol.*, 159: 645-651.

Ruzin, S.E. 1999. *Plant Microtechnique and Microscopy* (Vol. 198, p. 322). Oxford University Press, NY.

Schenk, H.J., S. Jansen and T. Hölttä. 2021. Positive pressure in xylem and its role in hydraulic function. *New Phytol.*, 230(1): 27-45.

Schrader, J., P. Shi, D.L. Royer, D.J. Peppe, R.V. Gallagher, Y. Li, R. Wang and I.J. Wright. 2021. Leaf size estimation is based on leaf length, width and shape. *Ann. Bot.*, 128: 395-406.

Seufert, P., S. Staiger, A. Bueno, M. Burghardt and M. Riederer. 2022. Building a barrier: The influence of different wax fractions on the water transpiration barrier of leaf cuticles. *Front. Plant Sci.*, 12: 766602.

Shah, S.M.R., S. Fatima, M. Hameed, S. Basharat, M.S.A. Ahmad, F. Ahmad, A. Asghar, M. Anwar, F. Yasmin, M. Ashraf and J. Shafqat. 2023. Allelochemicals extract of star–fruit (*Averrhoa carambola* L.) modulates wheat growth through alterations in anatomical architecture. *Crop Pasture Sci.*, 74: 423-437.

Sharma, A., B. Shahzad, V. Kumar, S.K. Kohli, G.P.S. Sidhu, A.S. Bali, N. Handa, D. Kapoor, R. Bhardwaj and B. Zheng. 2019. Phytohormones regulate accumulation of osmolytes under abiotic stress. *Biomolecules*, 9: 285-320.

Singh, A., M.D. Shamim and K.N. Singh. 2013. Genotypic variation in root anatomy, starch accumulation, and protein induction in upland rice (*Oryza sativa*) varieties under water stress. *Agric. Res.*, 2: 24-30.

Taylor, S., L. Kumar and N. Reid. 2012. Impacts of climate change and land-use on the potential distribution of an invasive weed: a case study of *Lantana camara* in Australia. *Weed Res.*, 52: 391-401.

Tester, M. and A. Bacic. 2005. Abiotic stress in grasses. From model plants to crop plants. *Am. Soc. Plant Biol.*, 137: 791-793.

Van Bel, A.J.E. and J.B. Hafke. 2005. Physiological determinants of phloem transport. In: (Eds.): Holbrook, N.M. and M.A. Zwieniecki. *Vascular Transport in Plants*. Burlington: Elsevier, pp: 19-44.

Vasellati, V., M. Oesterheld, D. Medan and J. Loreti. 2001. Effects of flooding and drought on the anatomy of *Paspalum dilatatum*. *Ann. Bot*., 88: 355-360.

Vendramini, F., S. Díaz, D.E. Gurvich, P.J. Wilson, K. Thompson and J.G. Hodgson. 2002. Leaf traits as indicators of resource-use strategy in floras with succulent species. *New Phytol.*, 154: 147-157.

Wagner, G.J., E. Wang and R.W. Shepherd. 2004. New approaches for studying and exploiting an old protuberance, the plant trichome. *Ann. Bot.*, 93: 3-11.

Yuan, F., B. Leng and B. Wang. 2016. Progress in studying salt secretion from the salt glands in recretohalophytes: How do plants secrete salt? *Front. Plant Sci*., 7: 1-12.

YuJing, Z., Z. Yong and H. ZiZhi. 2000. Studies on microscopic structure of *Puccinellia tenuiflora* stem under salinity stress. *Grassland China*, 5: 6-9.

Zhang, G., K. Cui, G. Li, J. Pan, J. Huang and S. Peng. 2022. Stem small vascular bundles have greater accumulation and translocation of non-structural carbohydrates than large vascular bundles in rice. *Physiol. Plant.*, 174: e13695.

Zhao, H.L., Y.H. He, G.Y. Yue and R.L. Zhou. 2010. Effects of wind blow and sand burial on the seedling growth and photosynthetic and transpiration rates of desert plants. *Chin. J. Ecol.*, 29: 413-419.

Zou, S., D. Li, N. Di, J. Liu, L. Li, Y. Liu, B. Xi and M. Coleman. 2022. Stand development modifies effects of soil water availability on poplar fine-root traits: Evidence from a six-year experiment. *Plant Soil*, 480(1): 165-184.

(Received for publication 18 March 2024)