

Morpho-anatomical variation between lowland and highland populations of *Cannabis sativa* L. in the Koh-e-Sulaiman and adjacent regions, Pakistan

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Abstract

Elevational gradients impose strong environmental constraints that alter plant structure and function. The study was conducted to compare morpho-anatomical variation in *Cannabis sativa* L. through a strong lowland-highland gradient (120-1770 m a.s.l.) in the Koh-e-Sulaiman region in Pakistan. The high-elevated populations (Fort Munro Lake, Fort Munro Road, and Fort Munro Hills) were of low temperature (6-8 °C), moderate precipitation (245-255 mm), and low soil salinity (ECe 1.21-1.34 dS m⁻¹), and the low-lands populations (Dera Ghazi Khan, Taunsa Sharif, and Shadan Lund) were of higher temperature (44-48 °C), less rainfall (170-210 mm), and higher salinity level. There were more morphological changes in the lowland populations, with longer root and shoot lengths, more leaves, and greater leaf area, compared with the highland populations, which tended to be shorter. Anatomical observations of ecotypes showed structural changes in plant parts. The plants in the highland exhibited more reinforced protective and regulatory tissues, such as increased cortical and endodermal layers in roots and increased epidermal thickness in the leaves, which showed structural changes towards a colder and fluctuating environment. In contrast, the lowland populations had increased lamina and mesophyll thickness, greater size of the vascular bundles, increased stomata number and size, and increased pith tissues, which caused the increased conductivity of water and its gaseous exchange in warmer and saline conditions. Statistical analyses showed that there is a significant difference in traits along the elevational gradient. These findings indicate strong phenotypic plasticity of *C. Sativa* in terms of morpho-anatomical adaptations that support the ecological adjustment of the species to both extreme climatic and edaphic conditions of the Koh-e-Sulaiman region.

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Introduction

High altitude vegetation is faced with a combination of abiotic limitations such as low temperature, low atmospheric pressure, high solar radiance, stormy winds, and limited available soil moisture. These environmental stresses cause extreme structural and functional changes in plants,

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and they often result in stunted or dwarf plant forms. Unfavorable weather conditions reduce the period of reproduction and early development of growth (Benitez-Alfonso et al., 2023). Of several defensive mechanisms, sclerification is regarded as the most prominent adaptive trait of grasses and other alpine plants, and it strengthens the mechanical properties and minimizes tissue damage in harsh environments, like those of the Himalayan region. Other anatomical features reported to aid survival in cold and moist climates are deep-seated bulliform cells, broader xylem vessel elements (Zahedi et al., 2025), and sclerified endodermis. Cold acclimation is a set of metabolic and structural changes, including alterations in gene expression, carbohydrate and protein concentrations, photosynthetic rate, and tissue structure, which contribute to increased freezing tolerance (Hassan et al., 2021).

Environmental stresses may strongly change plant development patterns, especially by modifying storage parenchyma, photosynthetic tissue, and conducting tissue, such as phloem, which is very sensitive to water shortage. Water scarcity can also lower the root and stem radii and the general leaf thickness. To avoid collapse and embolism, xylem elements usually grow narrower and more lignified in the area of water stress (Hassan et al., 2021). Plants have a process of phenotypic plasticity that alters morphology and structure by altering cell division, elongation, and differentiation (Li et al., 2021). These adaptations can be succulence, aerenchyma formation, vascular tissue enlargement, and sclerification (Fatima et al., 2023). Leaf-level adaptations, including increased thickness of the lamina, increased number of stomata, and hardened palisade and epidermal structures, increase drought resilience (Khan et al., 2023). Correspondingly, the thickening of sclerenchyma, the formation of a strong cuticle, and the alteration in the density of stomata can be helpful in the context of survival in the case of long-term water shortage (Saska et al., 2021).

Elevational gradients cause steep ecological changes within a geographically short distance, generating a rapid change in temperature, barometric pressure, solar radiation, and wind exposure and precipitation (Pepin et al., 2022). These gradients can provide powerful selection forces and cause morphological, anatomical, and physiological differences in plant populations. Despite overall genetic conservation of many of these anatomical structures across species, there is also a significant intraspecific change across elevation gradients that is typically linked to xeromorphic forms like smaller leaf size, increased sclerification, smaller and fewer stomata, stronger pubescence, and higher lignin deposition. Other approaches are adapted xylem vessel design, an increased photosynthetic rate at low temperatures, and thickened leaves (Shi et al., 2025).

Cannabis sativa is one of the first domesticated fiber and medicinal plants, which is used in the production of textiles, paper, building materials, nutraceutical oils, cosmetics, and pharmacologically active cannabinoid components such as THC and CBD (Sorrentino et al., 2021). Although the ecological range and economic significance of wild *C. sativa* populations are ecologically broad and economically significant, anatomical modifications of the wild *C. sativa* populations to elevational change are not well investigated in Pakistan.

The Koh-e-Sulaiman mountainous terrain of Dera Ghazi Khan is an example of a topographically diverse topography with lowland riparian settings, piedmont foothills, and upper rocky slopes with different climatic and edaphic conditions (Sajjad et al., 2024). The vegetation assemblages within this area have been found to correlate well with the elevation and related nutrient changes within the soil, causing a change in species richness and a switch in the community structure with changes in the gradient. Nevertheless, the morpho-anatomical strategies of adaptation to the ecological environment in *C. sativa* have not yet been studied within a consistent study across this elevation gradient. Hence, this study was conducted to evaluate the impacts of elevational gradient across a morpho-anatomical aspect of *Cannabis sativa* in the Koh-e-Sulaiman area, where the variation is not well understood.

Materials and Methods

Site selection

To study anatomical adaptations for the invasive success of *Cannabis sativa*, different populations were selected from low and high elevations in Koh-e-Sulaiman. The study sites were selected based on the occurrence of at least 10 populations per 500 m². The populations were selected from 123 m to 1970 m elevation. Environmental data was collected from the Pakistan Meteorological Department, Government of Pakistan, Head Office, stationed at Islamabad. Elevation above sea level was recorded using GPS (Garmin eTrex 10, USA).

Soil analysis

Rhizospheric soil near each plant (a total of 3 plants) was collected with a soil auger (10 cm) at three depths (15, 30, and 45 cm), mixed thoroughly to make one whole sample, and used for the measurement of soil physicochemical characteristics. Soil analyses were carried out in accordance with Handbook No. 60 (US Salinity Laboratory Staff, 1954). An extract from saturated soil paste was used for the estimation of pH and ECe using a pH/EC meter (WTW series InoLab pH/Cond 720, USA). Soil cations (Na, K, and Ca) were determined from the soil extract using a flame photometer (Jenway, PFP-7, UK). Soil Cl^- was measured with a digital chloride meter (Model 926, Sherwood Scientific Ltd., Cambridge, UK). Soil extract NO_3^- was measured spectrophotometrically, whereas soil PO_4^{3-} was measured using the Olsen method.

Plant selection

Three plants (one plant from each of three selected populations) were randomly selected at each study site for studying morpho-anatomical attributes, and treated as replications ($n = 3$). Since the exact age of natural populations was difficult to determine, the maximum plant height at the inflorescence stage and overall coverage (%) were used as selection criteria for sampling.

Morpho-anatomical parameters

Plants were uprooted carefully from the natural habitats and wrapped in a wet towel, and thereafter wrapped in a plastic sheath to minimize water loss through evapotranspiration. For the anatomical studies, root, stem, and leaf portions were fixed in formalin-acetic-alcohol (FAA) for 48 h. This was then shifted to an acetic alcohol solution for long-term storage. The free-hand sectioning method was used for the preparation of permanent slides through serial dehydration by ethanol. Biological stains, safranin and fast green, were used to develop a contrast between different tissue systems. An ocular micrometer was used for the anatomical measurements on a light microscope. Micrographs of stained sections were taken with a camera-equipped microscope (Nikon 104, Japan).

Statistical analysis

Data for each attribute was subjected to analysis of variance (ANOVA) followed by a Tukey's pairwise comparison test at a significance level ($p \leq 0.05$) for comparing the mean values. The standard error for each mean value was also calculated and presented on each bar.

Results

Weather

The average rainfall was 255 mm in Fort Munro Lake, 250 mm in Fort Munro Road, 245 mm in Fort Munro Hills, 170 mm in Shadan Lund, 202 mm in Taunsa Sharif, and 210 mm in Dera Ghazi Khan, respectively. The elevation increases in the following order: Dera Ghazi Khan (120 m), Taunsa Sharif (120 m), Shadan Lund (125 m), Fort Munro Hills (1700 m), Fort Munro Road (1750 m), and Fort Munro Lake (1770 m). The average maximum temperature increases in the following order: Fort Munro Lake (37 °C m), Fort Munro Road (37 °C m), Fort Munro Hills (37 °C m), Shadan Lund (44 °C m), Dera Ghazi Khan (44 °C m), and Taunsa Sharif (48 °C m). The average minimum temperature increases in the following order: Fort Munro Lake (6 °C m), Fort Munro Hills (7 °C m), Fort Munro Road (8 °C m), Taunsa Sharif (12 °C m), Shadan Lund (21 °C m), Dera Ghazi Khan (21 °C m) (**Figure 1**).

Soil physicochemical traits

The ECe was 1.21 dS m^{-1} in Fort Munro Lake, 1.34 dS m^{-1} in Fort Munro Road and Fort Munro Hills, 4.15 dS m^{-1} in Shadan Lund, 5.26 dS m^{-1} in Taunsa Sharif, and 5.98 dS m^{-1} in Dera Ghazi Khan, respectively. The soil pH was 8.3 at Fort Munro Lake, 8.2 at Fort Munro Road, 8.4 at Fort Munro Hills, 8.3 at Shadan Lund, 8.1 at Taunsa Sharif, and 8.6 at Dera Ghazi Khan, respectively. Organic matter in Fort Munro Lake was recorded as 0.53%, in Fort Munro Road as 0.64%, in Fort Munro Hills as 0.77%, in Shadan Lund as 0.73%, in Taunsa Sharif as 0.75%, and in Dera Ghazi Khan as 0.69%, respectively. The Soil Ca^{2+} in Fort Munro Lake was recorded as 31.12 mg kg^{-1} , in Fort Munro Road shows 30.01 mg kg^{-1} , in Fort Munro Hills 38.4 mg kg^{-1} , in Shadan Lund 116.3 mg kg^{-1} , in Taunsa Sharif 111.2 mg kg^{-1} , and in Dera Ghazi Khan it was 52.3 mg kg^{-1} , respectively (**Figure 2**).

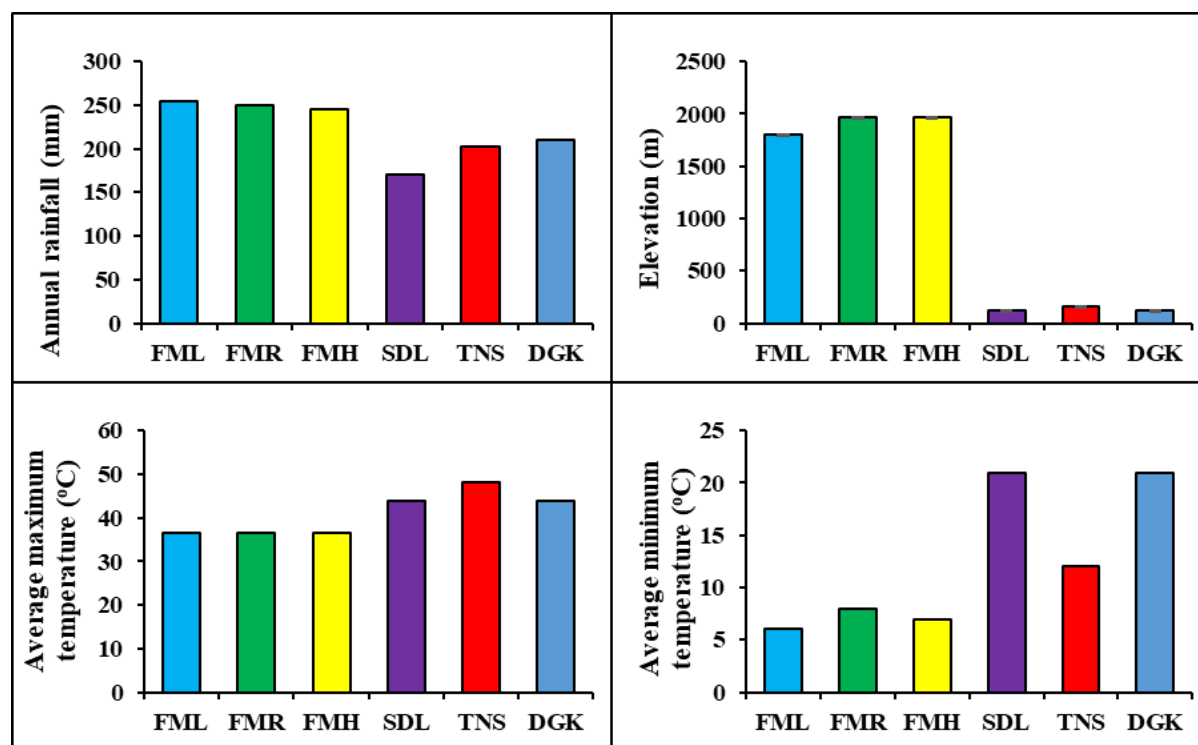


Figure 1: Weather data of Koh-e-Sulaiman and adjacent regions

Soil Data

The soil K⁺ in Fort Munro Lake was recorded as 84.64 mg kg⁻¹, in Fort Munro Road 78.8 mg kg⁻¹, in Fort Munro Hills 65.15 mg kg⁻¹, Shadan Lund 148.7 mg kg⁻¹, Taunsa Sharif 50.5 mg kg⁻¹ and in Dera Ghazi Khan 77 mg kg⁻¹, respectively. The Na⁺ in Fort Munro Lake was noted as 228.41 mg kg⁻¹, in Fort Munro Road 315.53 mg kg⁻¹, Fort Munro Hills 455.65 mg kg⁻¹, Shadan Lund 364.2 mg kg⁻¹, Taunsa Sharif 434.6 mg kg⁻¹, and in Dera Ghazi Khan as 555.1 mg kg⁻¹, respectively. The Cl⁻ in Fort Munro Lake was documented as 249.33 mg kg⁻¹, in Fort Munro Road 295.54 mg kg⁻¹, Fort Munro Hills 277.33 mg kg⁻¹, Shadan Lund 568.7 mg kg⁻¹, Taunsa Sharif 870.6 mg kg⁻¹, and in Dera Ghazi Khan 1398.5 mg kg⁻¹, respectively. The NO₃⁻ in Fort Munro Lake was recorded as 1.68 mg kg⁻¹, in Fort Munro Road 1.72 mg kg⁻¹, Fort Munro Hills 2.33 mg kg⁻¹, Shadan Lund 3.9 mg kg⁻¹, Taunsa Sharif 3.2 mg kg⁻¹, and in Dera Ghazi Khan as 2.8 mg kg⁻¹, respectively. The PO₄³⁻ in Fort Munro Lake was revealed as 6.64 mg kg⁻¹, in Fort Munro Road 7.96 mg kg⁻¹, Fort Munro Hills 8.21 mg kg⁻¹, Shadan Lund 15.7 mg kg⁻¹, Taunsa Sharif 16.1 mg kg⁻¹ and in Dera Ghazi Khan 9.6 mg kg⁻¹, respectively. The saturation percentage in Fort Munro Lake was documented as 38%, in Fort Munro Road 35%, Fort Munro Hills 39%, Shadan Lund 37%, Taunsa Sharif 36%, and in Dera Ghazi Khan 38%, respectively (Figure 2).

Morphological traits

Shoot length was the maximum (77 cm) in the Taunsa Sharif population (a lowland population), while the minimum (62 cm) was recorded in the Fort Munro Road population. In the other populations, shoot length increased in the following order: Fort Munro Hills 65 cm, Fort Munro Lake 68 cm, Shadan Lund 72 cm, and Dera Ghazi Khan 75 cm, respectively. Root length was the maximum (11 cm) in Taunsa Sharif (a lowland population), while the minimum (6 cm) was recorded in Fort Munro Lake. However, root length increased in the following order: Fort Munro Road 7 cm, Fort Munro Hills 8 cm, while Shadan Lund and Dera Ghazi Khan both showed 10 cm. The number of leaves per branch was recorded as 30 in Fort Munro Lake, Fort Munro Road 28, Fort Munro Hills 32, Shadan Lund 46, Taunsa Sharif 43, and Dera Ghazi Khan 45 (a lowland population), respectively. Leaf area was recorded as 78 cm² in Fort Munro Lake, 85 cm² in Fort Munro Road, 90 cm² in Fort Munro Hills, 134 cm² in Shadan Lund, 120 cm² in Taunsa Sharif, and 138 cm² in Dera Ghazi Khan, respectively (a lowland population) (Figure 3).

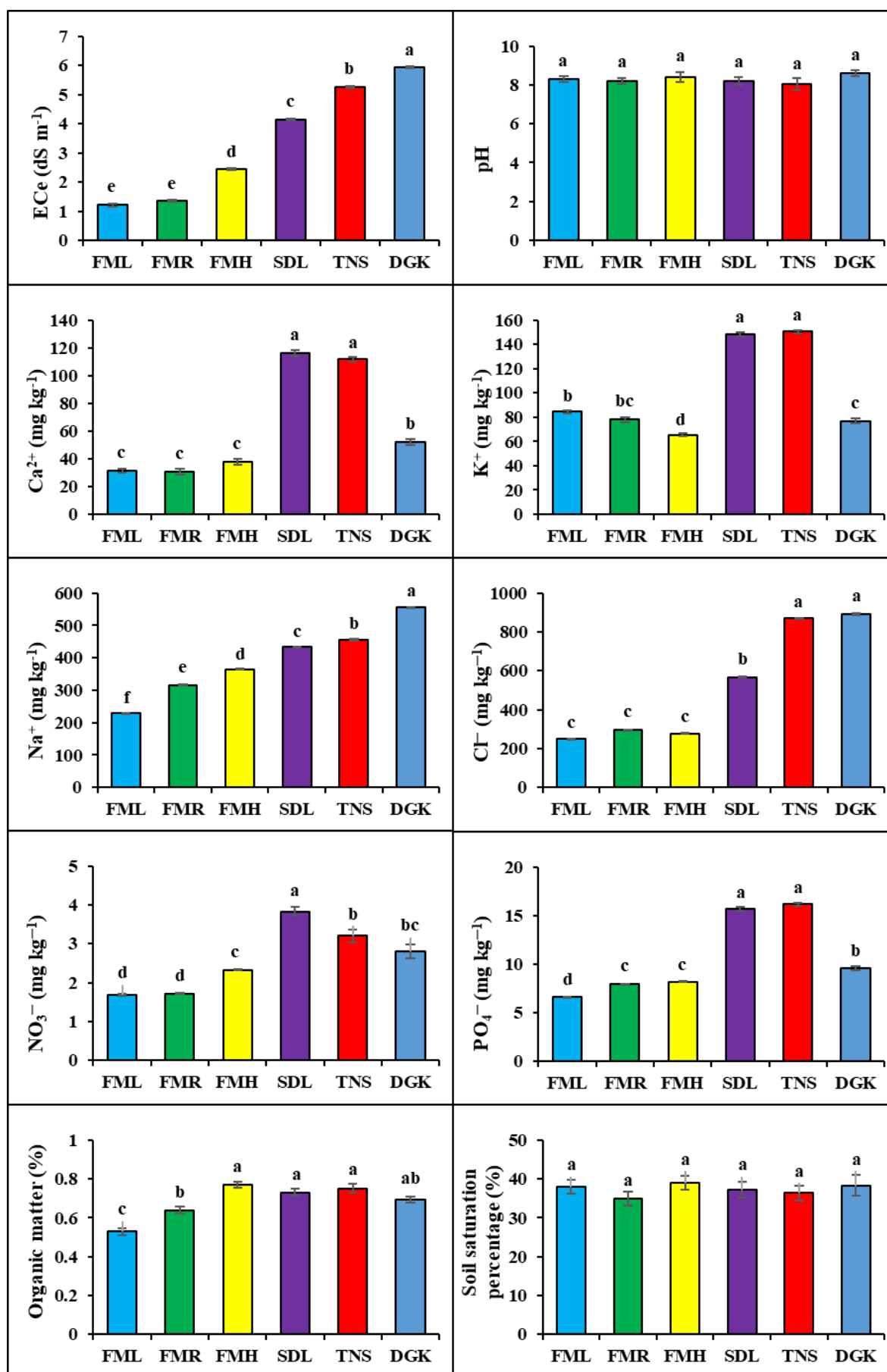


Figure 2: Physicochemical characteristics of the soil samples collected from Koh-e-Sulaiman and adjacent regions. Bars of each variable sharing the same alphabets do not differ significantly at $p < 0.05$.

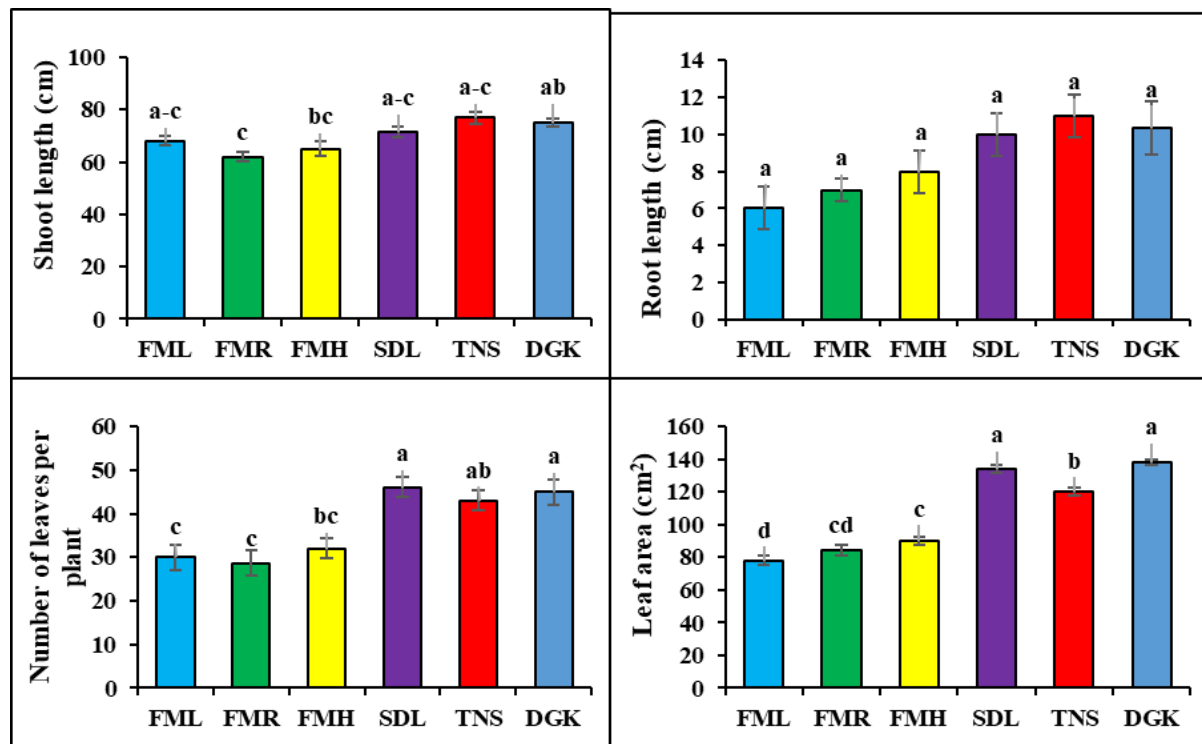


Figure 3: Morphological attributes of different *Cannabis sativa* populations from the Koh-e-Sulaiman and adjacent regions. Bars of each variable sharing the same alphabets do not differ significantly at $p < 0.05$.

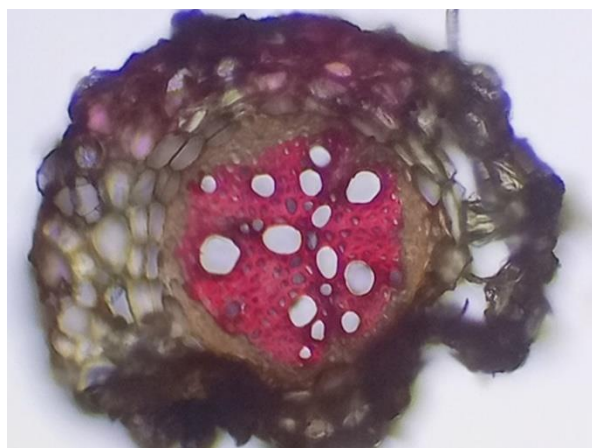
Anatomical Traits

Root Anatomy

The maximum root radius ($465.7 \mu\text{m}$) was recorded in Shadan Lund (a lowland population), while the minimum ($286.0 \mu\text{m}$) was observed in Dera Ghazi Khan (a lowland population). Regarding variations in root epidermal thickness, the maximum ($24.5 \mu\text{m}$) was observed in Fort Munro Road and Shadan Lund, while the minimum ($12.3 \mu\text{m}$) was recorded in Dera Ghazi Khan (a lowland population). The epidermal thickness decreased equally in Fort Munro Lake, Fort Munro Hills, and Taunsa Sharif. The maximum cortical region thickness ($187.9 \mu\text{m}$) was observed in Fort Munro Lake, while the minimum ($89.9 \mu\text{m}$) was observed in Dera Ghazi Khan (a lowland population). However, the cortical region thickness was much lower in Fort Munro Hills and Taunsa Sharif ($98.0 \mu\text{m}$) than that of the other populations examined in the current study. The endodermal thickness was the maximum ($32.7 \mu\text{m}$) in Fort Munro Lake, while the minimum ($16.3 \mu\text{m}$) was observed in Shadan Lund and Dera Ghazi Khan. The stellar region area was the maximum ($387048.3 \mu\text{m}^2$) in Shadan Lund (a lowland population), while the minimum ($90311.3 \mu\text{m}^2$) was observed in Fort Munro Lake. The maximum phloem thickness ($65.4 \mu\text{m}$) was observed in Fort Munro Road, while the minimum ($16.3 \mu\text{m}$) was observed in Shadan Lund (a lowland population). The phloem thickness was much lower ($24.5 \mu\text{m}$) in Fort Munro Hills and Dera Ghazi Khan (a lowland population) than that of other populations. The maximum metaxylem area ($3776.1 \mu\text{m}^2$) was observed in Fort Munro Lake, while the minimum ($839.1 \mu\text{m}^2$) was observed in Fort Munro Hills (**Figures 4-5**).

Stem Anatomy

The stem radius was the maximum ($473.9 \mu\text{m}$) in Fort Munro Hills, while the minimum ($359.5 \mu\text{m}$) was observed in Taunsa Sharif. The maximum epidermal thickness ($24.5 \mu\text{m}$) was observed in Taunsa Sharif, while the minimum ($16.3 \mu\text{m}$) was recorded in Fort Munro Road and Fort Munro Hills. The maximum cortical region thickness ($106.2 \mu\text{m}$) was observed in Fort Munro Lake, while the minimum ($57.2 \mu\text{m}$) was observed in Shadan Lund. The maximum phloem thickness ($65.4 \mu\text{m}$) was observed in Dera Ghazi Khan, while the minimum ($31.0 \mu\text{m}$) was observed in Fort Munro Lake. The maximum metaxylem area ($472.0 \mu\text{m}^2$) was observed in Taunsa Sharif. In comparison, the minimum ($262.2 \mu\text{m}^2$) was observed in Fort Munro Lake and Shadan Lund. The pith area and pith cell area were the maximum in Dera Ghazi Khan, while the minimum was recorded in Shadan Lund (**Figures 6-7**).



Fort Munro Lake: Reduced stellar region, large cortical cell area, sclerenchymatous cells in the stellar region



Fort Munro Road: Large cortical thickness, small metaxylem, distinct endodermis.



Fort Munro Hills: Reduced root radius, reduced metaxylem, no prominent endodermis



Shadan Lund: Reduced cortical thickness, large metaxylems, enlarged stellar region



Taunsa Sharif: Large stellar region, small endodermal thickness, large cortical thickness



Dera Ghazi Khan: Small epidermal thickness, small cortical thickness, large metaxylem area.

Figure 4: Root transverse section of *Cannabis sativa* collected from different regions of Dera Ghazi Khan Punjab, Pakistan

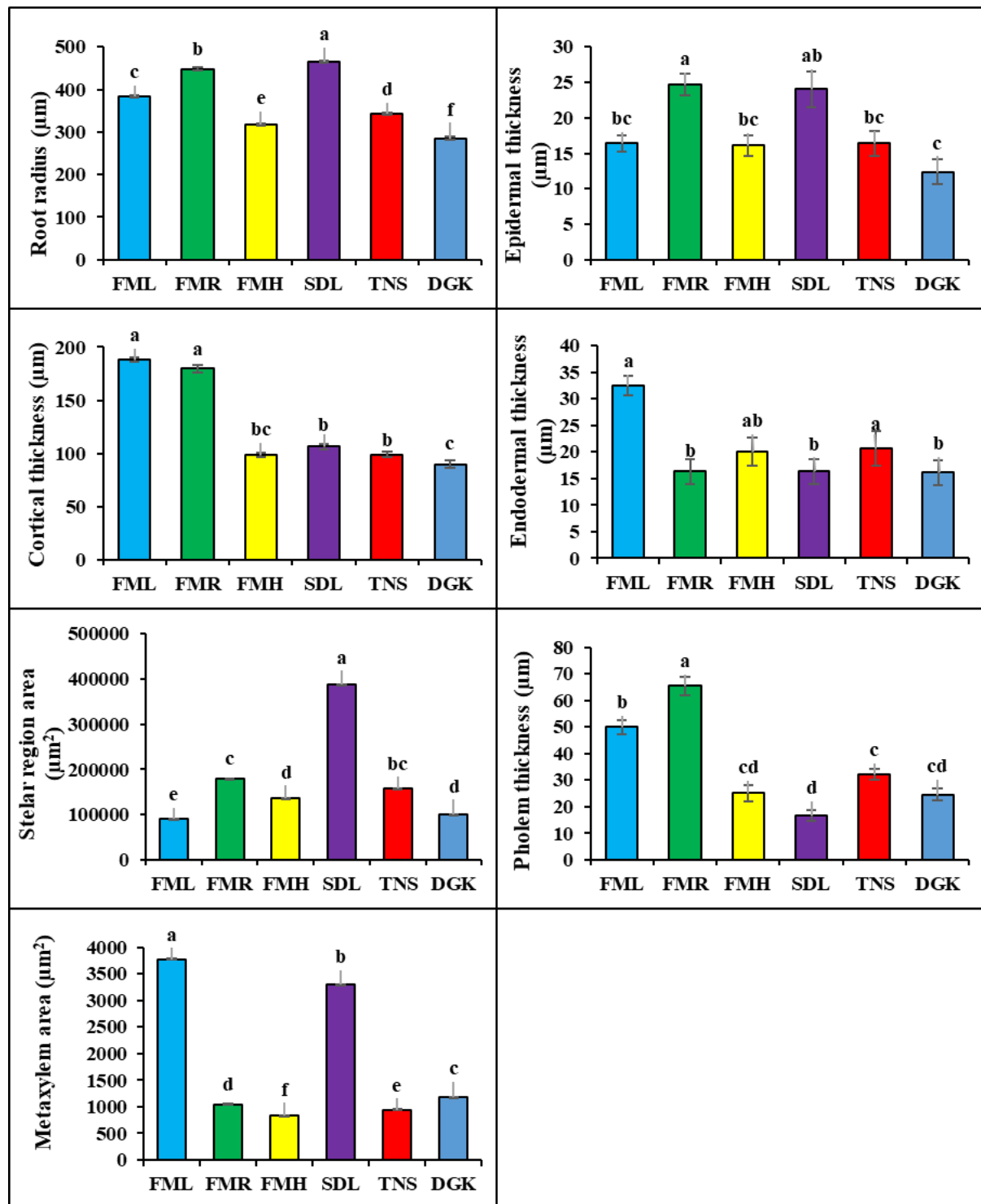
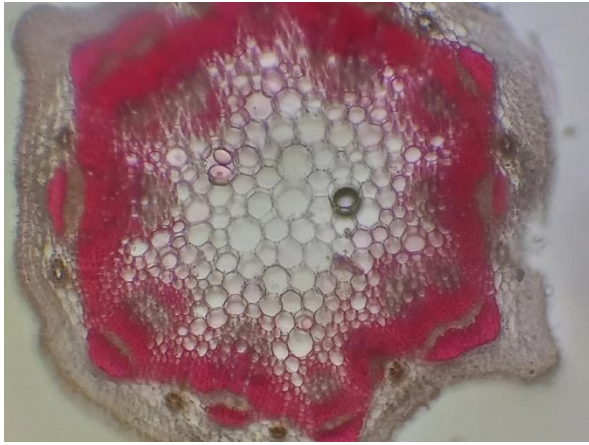
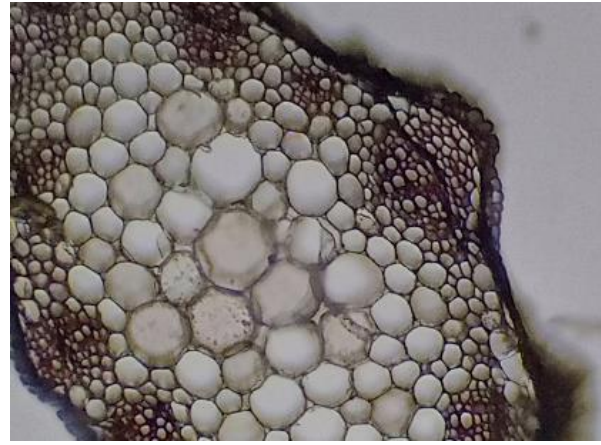


Figure 5: Root anatomical attributes of *Cannabis sativa* L. from the Koh-e-Sulaiman and adjacent regions. Bars of each variable sharing the same alphabets do not differ significantly at $p < 0.05$.



Fort Munro Lake: Small metaxylem area, large phloem thickness, small pith cells, and medium cortical thickness.



Fort Munro Road: Large pith cells area, small cortical thickness, distinct metaxylem area, and small phloem thickness.



Fort Munro Hills: Small cortical thickness, large pith cells, small epidermal thickness, large phloem thickness, and small vascular bundle area.



Shadan Lund: Small pith cell, large cortical thickness, distinct cuticles, and small pith area.



Taunsa Sharif: Large epidermal thickness, distinct metaxylem area, small phloem thickness, large cortical thickness, and large cuticle thickness



Dera Ghazi Khan: Large pith area, small pith cells, large cortical thickness, large epidermal thickness, and large vascular bundle.

Figure 6: Stem transverse sections of different populations of *Cannabis sativa* collected from the Koh-e-Sulaiman and adjacent regions

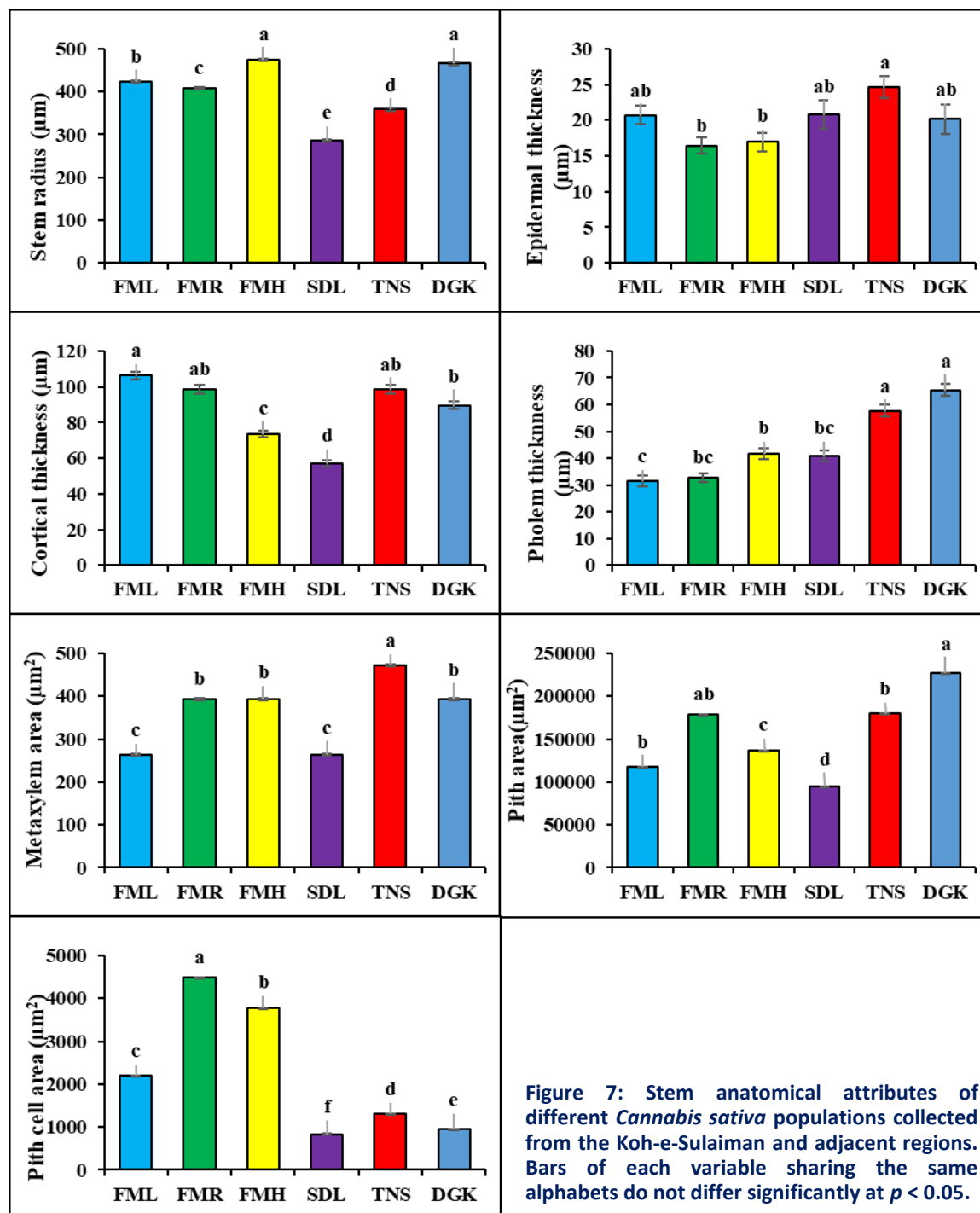


Figure 7: Stem anatomical attributes of different *Cannabis sativa* populations collected from the Koh-e-Sulaiman and adjacent regions. Bars of each variable sharing the same alphabets do not differ significantly at $p < 0.05$.

Leaf Anatomy

The midrib thickness was the maximum (547.4 μm) in Taunsa Sharif (a low elevation population), while the minimum (400.3 μm) was in Fort Munro Road (a high elevation population) (Figures. 8-11). The lamina thickness was the maximum (122.6 μm) in Taunsa Sharif (a low elevation population), while the minimum (57.2 μm) was in Fort Munro Lake (a high elevation population). The mesophyll thickness was the maximum (81.7 μm) in Taunsa Sharif (a low elevation population), while the minimum (32.7 μm) was in Fort Munro Lake (a high elevation population). The maximum cortical thickness (245.1 μm) was noted in Shadan Lund, a low elevation population, while the minimum (114.4 μm) was observed in Dera Ghazi Khan. The vascular bundle area was the maximum in Taunsa Sharif (54281.2 μm²), while the minimum (21397.8 μm²) was in Fort Munro Lake. The maximum phloem thickness (89.9 μm) was found in Shadan Lund, while the minimum (40.9 μm) was in Fort Munro Lake. The maximum metaxylem area (642.5 μm²) was observed in Taunsa Sharif, while the minimum (393.3 μm²) was in both Fort Munro Lake and Shadan Lund. The upper epidermal thickness was the maximum (24.4 μm) in Fort Munro Hills, while the minimum (16.3 μm) was in Shadan Lund.

The lower epidermal thickness was maximum (24.4 μm) in Fort Munro Lake, while the minimum (16.3 μm) was observed in both Fort Munro Hills and Shadan Lund. The number of stomata was the maximum in Dera Ghazi Khan, while the minimum was in Taunsa Sharif. The stomatal area was the maximum in Dera Ghazi Khan, while the minimum was in both Fort Munro Road and Taunsa Sharif (Figures 8-11).



Fort Munro Lake: Large cortical thickness, large number of leaf hairs, reduced phloem thickness, and large metaxylem area



Fort Munro Road: Maximum lamina thickness, small leaf hairs, and large vascular bundle



Fort Munro Hills: Large cortical thickness, large mesophyll thickness, small metaxylem area, and reduced leaf hairs



Shadan Lund: Large cortical thickness, reduced vascular bundle area, small lamina thickness, and large leaf hairs

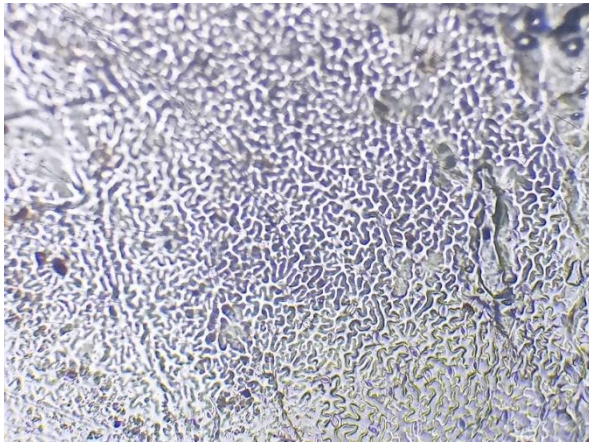


Taunsa Sharif: Large cortical thickness, reduced vascular bundle area, small metaxylem area, and large leaf hairs

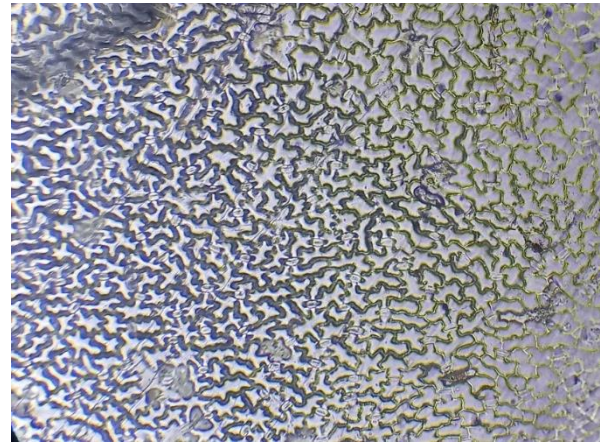


Dera Ghazi Khan: Reduced cortical thickness, small phloem thickness, small lamina thickness, and large metaxylem area

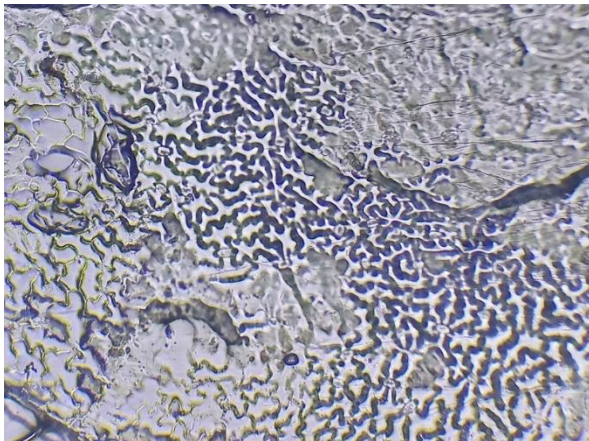
Figure 8: Midrib transverse sections of different *Cannabis sativa* populations collected from different regions of Dera Ghazi Khan, Punjab, Pakistan



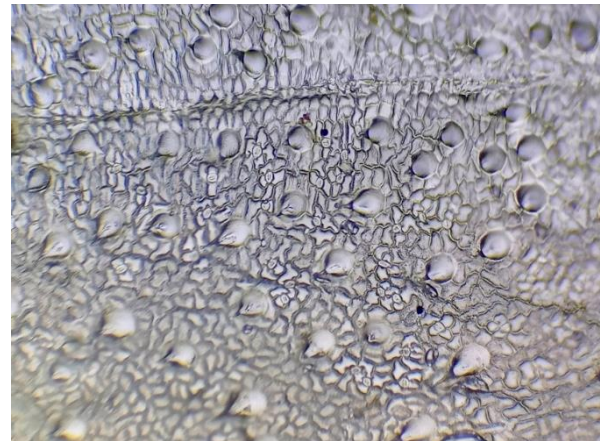
Fort Munro Lake: Maximum number of stomata, and small stomatal area



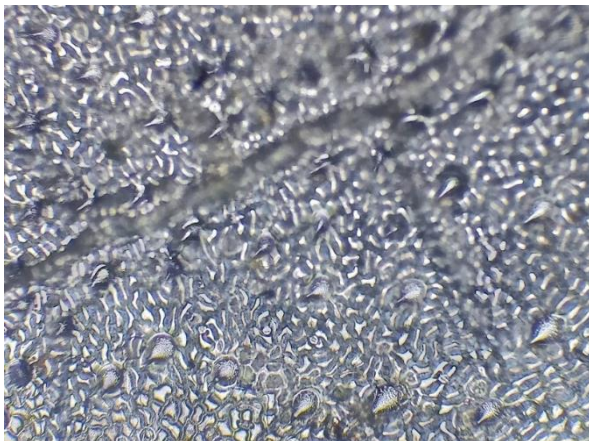
Fort Munro Road: Small stomatal area, and maximum number of stomata



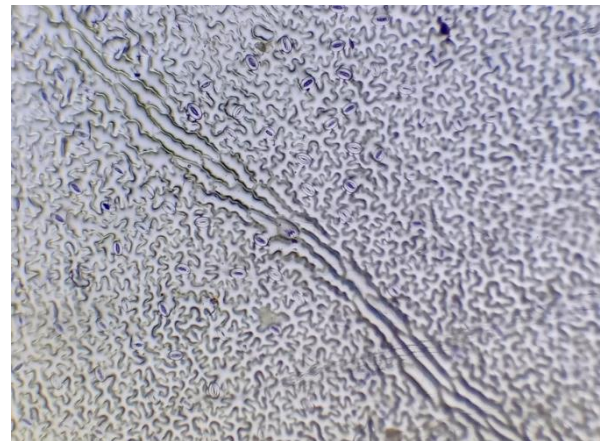
Fort Munro Hills: Small stomatal area, and a small number of stomata



Shadan Lund: Small number of stomata, and small stomatal area.

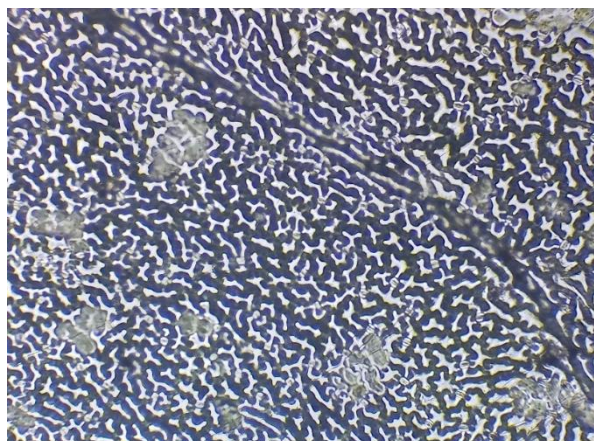


Taunsa Sharif: Small number of stomata, large stomatal area, and small leaf hairs

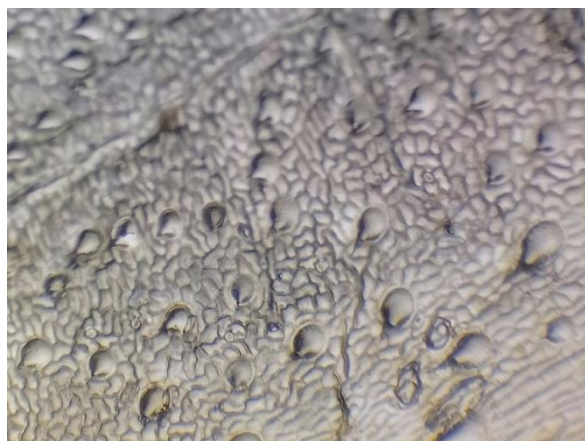


Dera Ghazi Khan: Dense number of stomata, and small stomatal area

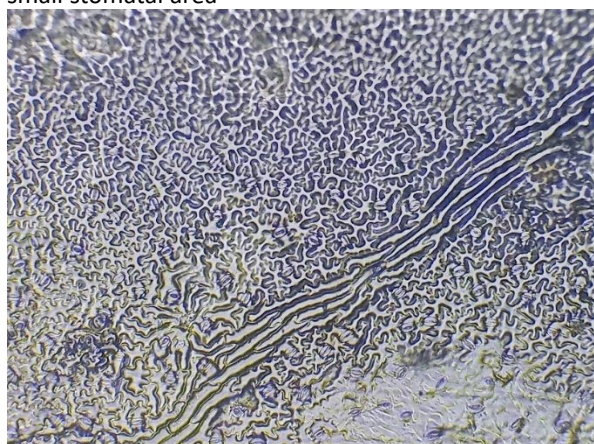
Figure 9: Anatomical characteristics of the upper epidermis of different *Cannabis sativa* populations collected from different regions of Dera Ghazi Khan, Punjab, Pakistan



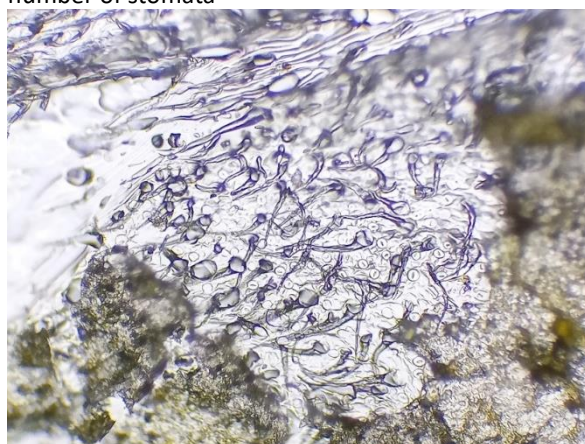
Fort Munro Lake: A dense number of stomata, and a small stomatal area



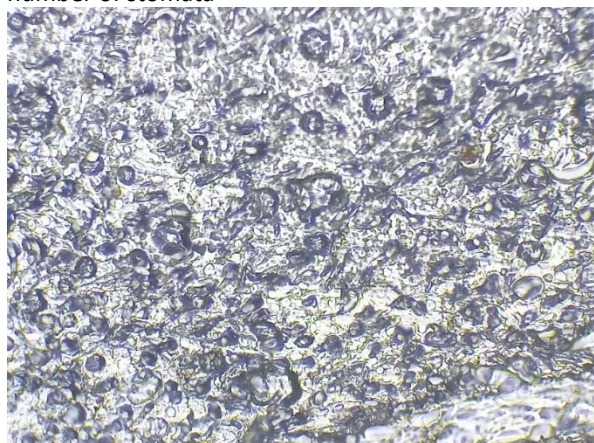
Fort Munro Road: A small stomatal area, and a small number of stomata



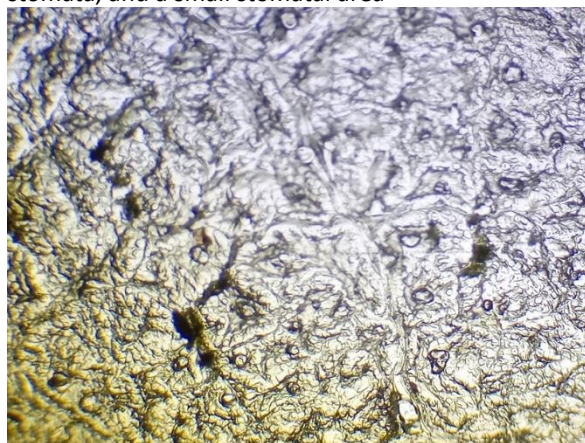
Fort Munro Hills: A small stomatal area, and a large number of stomata



Shadan Lund: Large leaf hairs, reduced number of stomata, and a small stomatal area



Taunsa Sharif: reduced stomatal area and a large number of stomata,



Dera Ghazi Khan; Reduced number of stomata, and a large stomatal area

Figure 10: Anatomical characteristics of the lower epidermis of *Cannabis sativa* populations collected from different regions of Dera Ghazi Khan, Punjab, Pakistan

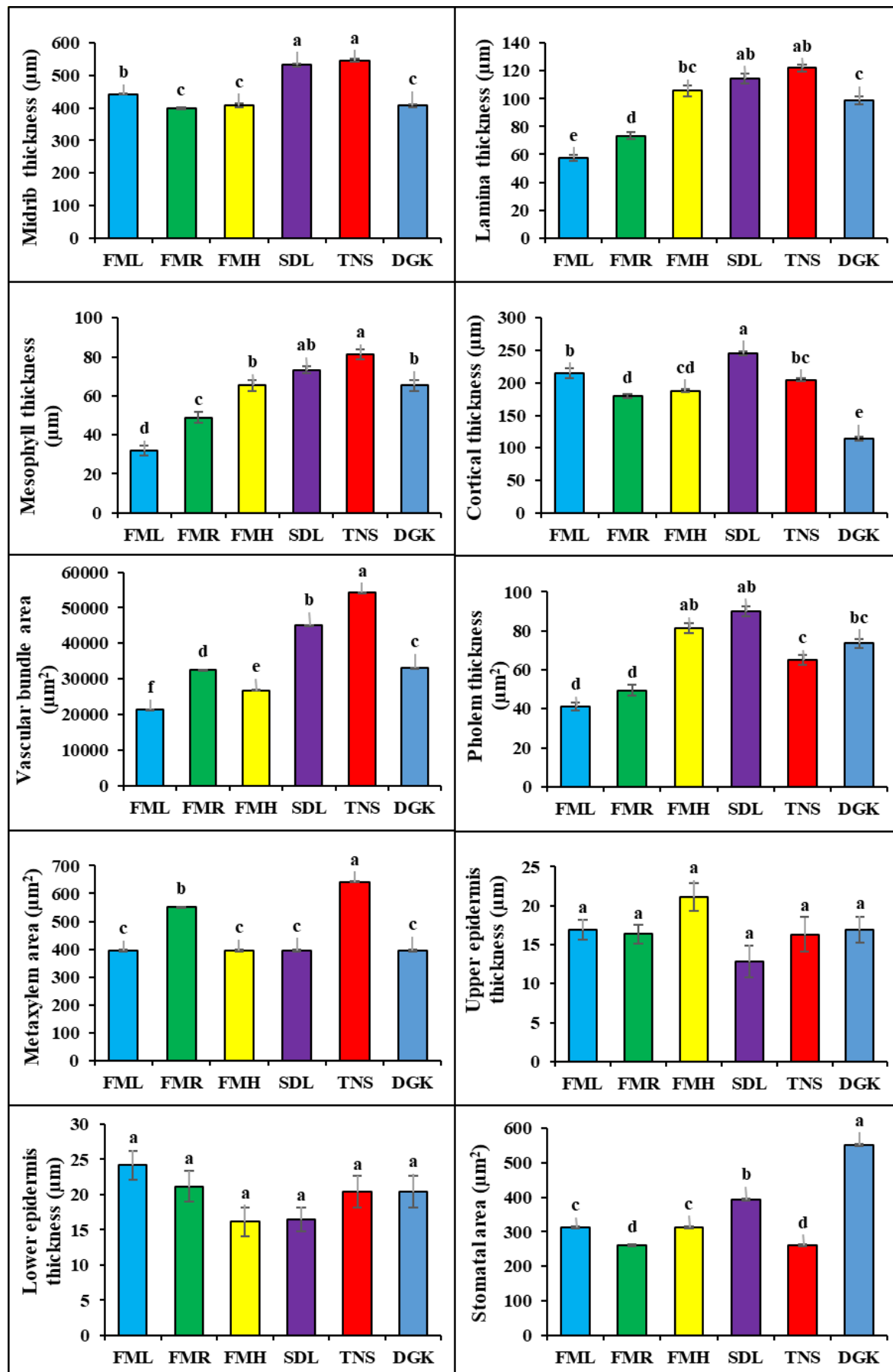


Figure 11: Leaf anatomical attributes of different *Cannabis sativa* populations from Koh-e-Sulaiman and adjacent regions. Bars of each variable sharing the same alphabets do not differ significantly at $p < 0.05$.

Discussion

Morpho-anatomical alterations of *Cannabis sativa* in the lowland-highland gradient of Koh-e-Sulaiman and adjacent areas seem to be closely linked to the environmental heterogeneity, such as elevation, temperature, precipitation, and soil chemistry. Highland populations (Fort Munro Lake, Fort Munro Road, and Fort Munro Hills) with an elevation of 1700-1770 m, had lower minimum temperatures (6-8 °C), moderate rainfall (245-255 mm), and soils with a relatively low electrical conductivity (1.21-1.34 dS m⁻¹), and medium nutrient content (Ca²⁺ 30-38 mg kg⁻¹; K⁺ 65-85 mg kg⁻¹). These circumstances were linked to structural adjustments that included an increase in the thickness of leaves, an augmentation of cortex and epidermis, and a fully developed metaxylem, which was in consistent with overall tendencies in plants where the thickness of leaves and stomatal density rise with elevation in reaction to lower temperatures, higher UV ray content, and water scarcity (Xiong et al., 2020).

Conversely, the populations of lowlands (Dera Ghazi Khan, Taunsa Sharif, and Shadan Lund) at 120-125 m had a greater exposure to a higher temperature, low rainfall (170-210 mm), and saline soils. Adaptation to such salinity stress has been reported as anatomical adjustments in plants, such as alterations in mesophyll, and this, together with changes in epidermal layers, has been observed as an adaptation strategy to balance water, in addition to alleviation of ion toxicity (Ouk et al., 2024). Also, the environmental research on *Cannabis sativa* has revealed that climatic gradients such as temperature and altitude have a strong impact on morpho-anatomical characteristics such as plant height, leaf area, and stem thickness, which are a phenotypic plasticity to environmental variation (Younas et al., 2024).

Plant architecture is highly regulated by environments based on the difference in the vegetative growth characteristics of *Cannabis sativa* in the lowland-highland gradient of the Koh-e-Sulaiman region. The populations of Taunsa Sharif (lowland) and Dera Ghazi Khan had the highest length of shoots, and the height of the shoots was lower in highland populations, including Fort Munro Road and Fort Munro Hills. A decreasing stature of vegetation with increasing altitude is an ecologically established phenomenon and is generally explained by low temperature, short growing periods, and high abiotic stress (Masoud et al., 2025). The main reason is that alpine and high-elevation vegetation often has a limited growth in an adaptive response to thermal constraints and wind exposure (James et al., 2026).

Root length also exhibited the same trend, with the root growth being more in the lowland populations than in the highland populations. Root growth and general biomass distribution are highly affected by temperatures, and colder soils tend to favour greater root growth (Li et al., 2023). Also, the ratios between roots and shoots may also change under the influence of environmental stress gradients, which influences the overall architecture of a plant (El Amrani, 2023).

There was also a strong variation in leaf production and the leaf area. The population of the lowlands had more leaves and a much greater leaf area compared to the highland populations. Greater loss of leaf area with higher elevation has been widely documented and commonly explained as an adaptation to promote a more economical use of transpirational water evaporation and coping with cooler and higher-radiation climates (Xiong et al., 2020; Pranatami et al., 2023). Smaller leaves also have a positive heat balance and mechanical stability in an environment under stress (Hassan et al., 2022).

Cannabis sativa still exhibited relatively robust growth in shoot and root despite the increased salinity in lowland locations. Salinity normally causes osmotic and ionic stress, which inhibits growth in most plant species (Munns and Tester, 2008). But some species show a significant phenotypic plasticity under moderate saline conditions, which adapt the growth patterns and remain able to produce biomass (Assaeed et al., 2023). Morpho-anatomical studies have also revealed that climatic and edaphic gradients have strong effects on morpho-anatomical traits, like the height of the *Cannabis sativa*, leaf size, and branching patterns, which further validate the susceptibility of the *Cannabis sativa* to the environmental heterogeneity (Ghosh et al., 2024).

The difference in the anatomical characteristics of roots in the populations studied reflects the ecological insight of lowlands (Dera Ghazi Khan and Shadan Lund) and highlands (Fort Munro Road, Fort Munro Lake, and Fort Munro Hills). Root anatomical plasticity is a well-established adaptive response that allows plants to adapt to the varying soil moisture, temperature, and edaphic stress (Shah et al., 2026). The root radius was larger in Shadan Lund, which could lead to better exploration of soil and hydraulic conductivity in the changed lowland conditions (Webb et al., 2022), but the radius in Dera Ghazi Khan was smaller, suggesting structural adaptation to the stress factors in the

area (Ranjan et al., 2022). The epidermal thickness is higher in Fort Munro Road and Shadan Lund, which is probably an adaptive mechanism that offers mechanical protection and minimizes environmental harm, also typical of stress tolerance (Basharat et al., 2024).

The cortical and endodermal thickness were the greatest in Fort Munro Lake, which suggested enhanced internal storage and selective regulation of ions (Abid et al., 2026). It is often also associated with thickening of these tissues, which enhances the control of water and solute movement in the face of environmental stress (Zahedi et al., 2025). Conversely, the occurrence of thinner cortical and endodermal areas in Dera Ghazi Khan could be indicative of less structural investment in conditions of relatively stable lowlands (Fatima et al., 2026). The increase in stellar area in Shadan Lund implies that there is greater vascular transport efficiency and augmented thickness in the phloem (Shah et al., 2025) in Fort Munro Road, and augmented metaxylem area in Fort Munro Lake indicates that there are adaptive modifications in assimilate and water movement (Imran et al., 2024). In general, the populations in highlands were more likely to have thicker protective and conductive tissues, which would help them adjust to cooler and possibly moisture-fluctuating climate conditions, whereas the populations in lowlands were more likely to have features that would help them to efficiently acquire their resources in warm weather (Pranatami et al., 2023).

The anatomical differences of stems in the examined populations can be noted to show clear structural differences with elevational and environmental gradients between lowland (Dera Ghazi Khan, Shadan Lund, and Taunsa Sharif) and highlands (Fort Munro Hills, Fort Munro Lake, and Fort Munro Road). The process of stem structural plasticity is commonly considered to be an adaptive reaction to the ecological stress that affects mechanical support, hydraulic efficiency, and storage capacity (Liu et al., 2025). A lower value of the stem radius of Fort Munro Hills implies increased mechanical strength, which is usually beneficial in highland habitats that experience greater winds and variable weather conditions (Fatima et al., 2026). Enhanced stem diameter is usually linked to advanced structural stability, as well as conductive capacity (Iqbal et al., 2026). Conversely, the lesser size of the stem radius in Taunsa Sharif can be an indicator of a lower level of structural investment in relatively lower exposed conditions (Naveed et al., 2023).

Epidermal thickness was highest in Taunsa Sharif, which implies that the outer protective tissue is stronger. If the epidermis is thicker, it may decrease transpiration and offer resistance to environmental stress like heat and desiccation (Yavas et al., 2024). On the other hand, epidermal layers in Fort Munro Road and Fort Munro Hills were thinner and, therefore, could indicate varying adaptive priorities, perhaps giving importance to internal tissue growth (Shahid et al., 2025). All other places had the least cortical thickness at Fort Munro Lake and the greatest at Shadan Lund. Growth of cortical tissues may increase mechanical support and short-term storage, especially in environments prone to environmental changes. Higher cortical development is associated with higher tolerance to stressful circumstances (Iqbal et al., 2025).

The phloem thickness was highest in Dera Ghazi Khan, implying that in lowland conditions, active growth could be promoted by a higher capacity of assimilate transport. The modification in the growth of phloem is commonly linked to the carbon allocation efficiency and environmental adaptation (Liang et al., 2023). Equally, the greater metaxylem area at Taunsa Sharif represents a higher hydraulic conductivity, and the smaller metaxylem area at Fort Munro Lake and Shadan Lake could be a case of conservative hydraulic transport strategy (Li et al., 2023). The much larger pith and pith cell area of Dera Ghazi Khan indicates a higher internal storage and structural buffering capacity, which can assist in growth under warmer lowland conditions. The stem flexibility and water and metabolite storage are commonly linked to pith development (Jing et al., 2025). Overall, highland and lowland populations tended to be characterized by structural and anatomic traits, respectively. These coordinated changes in stems can be considered as anatomical plasticity in response to environmental heterogeneity across habitats.

Anatomical differences of the leaves of the populations under study indicate noticeable altitudinal variations without differences between low-elevation sites (Taunsa Sharif, Shadan Lund, and Dera Ghazi Khan) and high-elevation sites (Fort Munro Road, Fort Munro Lake, and Fort Munro Hills). Leaf structure is very plastic, and it is closely interconnected with the environmental conditions like temperature, irradiance, and the availability of moisture (Ma et al., 2025). The increased values of midrib and lamina in Taunsa Sharif (low elevation) would indicate a high level of mechanical support and photosynthetic tissues in a warmer environment. The dense lamina and mesophyll thickness tend to be associated with the enhancement of the photosynthetic ability and water retention capabilities (Luo et al., 2023). On the contrary, the decreased lamina and mesophyll thickness of the Fort Munro Lake (high elevation) could be an adaptation to colder climates and

possibly shorter growing seasons, whereby thin leaf construction costs less.

Taunsa Sharif also had a greater vascular bundle area and metaxylem formation, and so is better at transporting water in lowland thermal conditions, which is associated with a high hydraulic efficiency. Vascular tissue expansion is usually linked to enhanced water conduction and assimilate movement (Iqbal et al., 2026). On the other hand, the existence of smaller vascular tissues in Fort Munro Lake indicates a conservative hydraulic approach. Shadan Lund showed the greatest thickness of phloem, which suggests that it may have translocated assimilates higher in lowlands. The range of phloem development variability is usually connected with the carbon distribution approaches and developmental processes (Li et al., 2026).

The pattern of epidermal thickness was the opposite, where the upper epidermis was thicker in Fort Munro Hills, and the lower epidermis was thicker in Fort Munro Lake. The increased radiation intensity, temperature range, and desiccation could be insulated by a thickened epidermal cover on elevated levels (Fatima et al., 2026). Stomatal characteristics also aid in ecological separation. The greater stomatal count and stomatal area in Dera Ghazi Khan (low altitude) indicate increased capacity of gas exchange, which would provide increased photosynthetic demand at warmer temperatures. Adaptive traits well documented include stomatal density and size as a result of the environmental gradients, especially temperature and water availability (Wang et al., 2022).

Overall, the lowland population had thicker photosynthetic tissues, large vascular structures, and more stomatal investment, suggesting that it is adapted to high hydraulic conductivity and carbon uptake. Highland populations, in contrast, exhibited more modest changes in lamina thickness but epidermal fortification in line with structural adaptations to either colder or more stressful climatic conditions. These anatomical adaptations show altitudinal adaptive plasticity in these coordinated modifications of leaves.

Conclusion

In the current study, the populations of *Cannabis sativa* along the Koh-e-Sulaiman elevation axis were characterised by a pronounced morpho-anatomical differentiation related to opposing climatic and edaphic conditions. The lowland populations, which were exposed to heat and salinity of the soils, exhibited higher vegetative growth, thicker photosynthetic tissues, larger vascular elements, and more stomatal investment, which were indicative of adaptive strategies of hydraulic effectiveness and carbon sequestration at temperatures and salinity under thermal and ionic stress. Conversely, populations with long distances to the equator (highlands) were typified by cooler conditions and moderate precipitation that manifested retarded structural tissues, including increased cortical, endodermal, and epidermal layers, indicating the development of anatomical adaptations to stabilize mechanical traits and regulate water and ionic balance. These coordinated modifications of roots, stems, and leaves affirm the fact that *C. sativa* has a high degree of phenotypic plasticity; as such, it can survive at steep ecological gradients. The results offer a new understanding of adaptive structural strategies of wild *C. sativa* in Pakistan and the ecological importance of the elevational heterogeneity in developing intra-specific variation. This knowledge can also be used in the future as a source of conservation, ecology, and possible breeding approaches to stress resilience in this economically valuable species.

Author(s), Editor(s) and Publisher's declarations

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Contribution of authors

Research supervision: AH and SMRS. Conceptualization and designing the study: AH, SMRS, SSZN. Conduction of experiment: JS, AH. Resource availability: ZP, WR. Moderation of laboratory activities: AZ, ZA, BA. Instrumentation and analysis: BA, SFN, LH, SA. Preparation of initial draft: SMRS, AZ. Revision of final draft and proofreading: All authors.

Permissions and ethical compliance

This study does not involve human/animal subjects, and thus no ethical approval is required.

Handling of bio-hazardous materials

The authors certify that all experimental materials were handled with great care during collection and experimental procedures. After completion of the study, all materials were properly discarded to minimize/eliminate any types of bio-contamination(s).

Supplementary material

No supplementary material is included with this manuscript.

Conflict of interest

The authors declare no conflict of interest.

Availability of primary data and materials

As per editorial policy, experimental materials, primary data, or software codes are not submitted to the publisher/Journal management. These are available with the corresponding author (s) and/or with other author(s) as declared by the corresponding author (s) of this manuscript.

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