

Elevation-driven morpho-anatomical adaptations in *Withania coagulans* (Stocks) Dunal from the Koh-e-Suleiman highlands

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Abstract

Elevational gradients form highly effective environmental filters that determine the morphological and internal pathways of plants, leading to adaptive changes in natural populations. *Withania coagulans* (Stocks) Dunal is an ecologically and medicinally valuable species commonly growing throughout the Koh-e-Suleiman Highlands of Pakistan, but its altitude-associated adaptive compensations are not well understood. This paper examined morphological and anatomical diversity in the populations of *W. coagulans* that varied in terms of altitudes with an aim of explaining structural adaptations in the face of environmental differences. Morphological parameters such as root length, plant height, leaf area, and number of leaves per branch had high site-specific variance, with maximum growth performance observed in the Lundi Saidan population and minimum growth performance seen in the Fort Munro Road population due to variation in environmental constraints in terms of altitude and temperature. Root anatomical characteristics, including epiblema thickness, cortical thickness, metaxylem area, endodermal thickness, and root radius, exhibited different patterns of adaptations with respect to efficiency of water uptake and ionic regulation. Stem structural characteristics brought about a variation in epidermal thickness, cortical thickness, vascular tissue, pith area, and stem radius as evidence of mechanical support and internal water storage. Further functional adaptations that were not previously mentioned regarding transpiration regulation and hydraulic conductivity were also revealed by leaf anatomical characteristics such as epidermal thickness, midrib thickness, vascular bundle area, metaxylem area, and stomatal density. The presence of both morphological and anatomical responses suggests a high level of phenotypic plasticity of *W. coagulans*, which allows populations to maximize growth, regulate water relations, and hence, tolerance to stress conditions along elevation gradients. These results provide new information about the adaptive structural solutions to highland medicinal flora and provide a scientific foundation for conservation planning and habitat-specific culture of *W. coagulans* in mountainous areas.

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Introduction

The ecology of mountain ranges is highly heterogeneous in terms of the environment. Steep elevations create high selective pressures on the growth, structure, and survival of plants. The difference in temperature, precipitation, atmospheric pressure, solar radiation, and soil properties among the elevations has a considerable impact on the distribution of plants, their physiology, and anatomy (Shah et al., 2025; Fatima et al., 2026). Therefore, to investigate the adaptive behavior of plants to various abiotic stresses, elevational gradients offer a natural system to consider.

The Koh-e-Suleiman region is a significant physiographic division of the Suleiman fold belt in the middle of the Indus Basin in Pakistan. This area has a link between dry lowland plains and mountainous relief, and it covers a high diversity of heights in a short distance of geographical location (Larsen et al., 2014). Dera Ghazi Khan is at the eastern foot of the Koh-e-Suleiman Range, and it is a climatically delicate transition zone between the Indus plains and upland ecosystems. Climate extremes, such as heavy monsoon rains, flash floods, extended droughts, and rising temperature variability, are very dangerous to the region (Ur Rehman Naseer et al., 2025). The recent climate anomalies and especially the disastrous monsoon floods of 2022 point to the growing ecological pressure on vegetation in the southern Punjab and neighboring mountainous areas (Chandel, 2025).

The Koh-e-Suleiman region is characterized by complicated relations between elevation (maximum elevation about 3,487 m), climate, edaphic factors, and vegetation. Although there is a variety of plants at higher elevations, the xerophytic and desert-adapted plants dominate lower elevations (Toderich et al., 2007). Despite this ecological significance, there are limited quantitative studies that have associated the structural adaptations of plants with elevational gradients of the dry mountainous areas in Pakistan, which is also attributable to remoteness and inaccessibility (Haq et al., 2024). Consequently, little is known about geo-climatic stressor responses by plants in this area.

Elevation puts several stresses on vegetation, such as low temperature, low atmospheric pressure, low oxygen levels, and increased ultraviolet (UV) radiation (Körner, 2002). All these factors restrict photosynthesis, respiration, and the growth rate, which, in many cases, are accompanied by anatomical adaptations in the form of lower leaf area, increased tissue thickness, more sclerenchyma development, and a restructuring of the vascular network (Oguchi et al., 2018). It has been reported that conducting tissues, especially xylem and phloem, have reductions in their size and number with increasing elevation, which could increase resistance to freeze-induced embolism and mechanical stress (Mayr and Améglio, 2016; Li et al., 2023).

Drought and salinity stresses usually accompany elevational stress in arid and semi-arid mountainous systems. The issue of water shortage lessens the expansion of the leaves, stomatal conductance, and photosynthetic effectiveness, whereas it promotes the growth of deeper roots and larger areas of sclerenchymatous tissues as water reservoirs (Li et al., 2023). Salinity also contributes to physiological drought through lowering the water potential of soils and causing ionic toxicity, necessitating adaptation mechanisms to salt through the use of ion compartmentalization, osmolyte accumulation, and specialized leaf morpho-anatomical structures (Abrar et al., 2020; Ma et al., 2020).

The range of adaptive characteristics of xerophytic species in the Koh-e-Suleiman area includes thick cuticles, high stomatal resistance, small leaf area, compact epidermal cells, and well-developed vascular tissues, which contribute to their overall success in surviving harsh environmental conditions (Bano et al., 2019). Thus, this type of eco-morphological and anatomical plasticity is important for plant performance under changing stress regimes.

Withania coagulans (Stocks) Dunal is one of the xerophytic shrubs in the Solanaceae family that is endemic to Pakistan, Iran, Afghanistan, and India, and is medicinally important (Yasmin et al., 2025). The species is prized due to its highly phytochemical compounds, especially withanolide, that have antimicrobial, anti-inflammatory, antihyperglycemic, hepatoprotective, and antioxidant effects (Khan et al., 2021; Yasmin et al., 2025). Although *W. coagulans* has ecological and pharmacological significance, very little is known about the impact of elevational gradients on the anatomical structure of the plant, especially in arid mountainous habitats.

Considering the growing intensity of the stresses caused by climate and the ecological importance of the Koh-e-Suleiman region, it is timely to examine which anatomical adaptations to elevation occur in *W. coagulans*. The current research paper tended to explain the variation in anatomical characteristics of *W. coagulans* across an elevational gradient in the Koh-e-Suleiman area, which could shed light on structural mechanisms that facilitate plant survival in high altitude, as well as water scarcity and salinity stress. The results provide a background on the study of the resilience

of plants in arid mountainous regions and the conservation and sustainable use of medicinal plants.

Materials and Methods

Plant collection and study area

A field survey was conducted in ecologically different areas of Punjab to obtain naturally adapted populations of *Withania coagulans*. The sampling sites were chosen to represent different environmental conditions, such as the plains, dry zones, and mountainous areas. The plant material was picked directly from the natural habitats in the Koh-e-Suleiman Range, that is, Sakhi Sarwar Road, Fort Munro Road, Sakhi Sarwar Pul, Lundi Saidan, and Dara Kaha. Plant samples were freshly collected during the growing season when plants were active, and taken to the laboratory for morphological, anatomical, and physiological tests.

Anatomical studies

In the case of anatomical analyses, stem branches and adventitious roots were cut off into about 3 cm-long segments. Immediately, the samples were fixed in formalin-acetic acid-alcohol (FAA; v/v: formalin 10%, acetic acid 5%, ethanol 50%, distilled water 35%) for 48 h, and then the samples were transferred to acetic alcohol solution (v/v: acetic acid 25%, ethanol 75%) to store the samples long-term. Freehand transverse sections were developed, and a double-staining procedure was done with safranin and fast green. Permanent slides were made according to the peeled-off procedure as given by Naz et al. (2022) and Ruzin (1999). Microphotography, anatomical observations, and measurements were made using a camera-equipped microscope (Meiji Techno, Japan). An ocular micrometer with a calibration using a stage micrometer was used to do the quantitative measurements.

Statistical analysis

All data were analyzed using analysis of variance (ANOVA), and thereafter, a pair-wise comparison of means was done using Tukey's test at $p < 0.05$. The ggcorrplot and ggplot2 packages were used to compute correlation matrices in R statistical software (R Core Team, 2019). RDA was conducted in order to assess the correlation between morphological and anatomical characteristics with CANOCO version 5 in Windows.

Results

Weather data

The maximum average rainfall was recorded at Fort Munro Road (FMR; 250.52 mm), while the minimum was at Lundi Saidan (LSD; 70.53 mm). The maximum elevation was noted at Fort Munro Road (1800.58 m), while the minimum elevation was at Lundi Saidan (154.55 m). The maximum average temperature was at Sakhi Sarwar Road (SSR), Sakhi Sarwar Pul (SSP), and Lundi Saidan, while the minimum average temperature was recorded at Fort Munro Road (37.3 °C). The maximum of the average minimum temperature was observed at Lundi Saidan (21.4 °C), while the minimum of the average minimum temperature was observed at Fort Munro Road (7.4 °C) (**Table 1**).

Table 1: Environmental characteristics of the studied habitats showing rainfall, elevation, maximum temperature, and minimum temperature.

Habitat	Rainfall (mm)	Elevation (m)	Max. Temp (°C)	Min. Temp (°C)
LSD	70.53 ± 1.98	154.55 ± 4.94	42.2 ± 0.97	21.4 ± 0.91
SSP	90.58 ± 2.08	284.49 ± 5.1	42.3 ± 0.94	21.4 ± 0.99
SSR	90.31 ± 1.95	290.42 ± 4.92	42.4 ± 0.96	21.2 ± 0.98
DKA	88.25 ± 1.94	380.57 ± 5.09	40.5 ± 0.93	20.3 ± 0.98
FMR	250.52 ± 5.06	1800.58 ± 9.98	37.3 ± 0.94	7.4 ± 0.93

Soil analysis

The maximum electrical conductivity (ECe) of soil samples as saturated paste was recorded in Lundi Saidan (2.15 dS m⁻¹), while the minimum was recorded in Sakhi Sarwar Pul habitat (1.09 dS m⁻¹) (**Figure 1**). The maximum pH was observed at Sakhi Sarwar Road (8.33), while the minimum was at Dara Kaha (8.1). The organic matter was highest in Lundi Saidan (0.80%), while it was the lowest in Dara Kaha (0.62%). The maximum Ca²⁺ concentration was observed in Sakhi Sarwar Road (45.5 mg L⁻¹).

¹), while the minimum was found in Fort Munro Road (30.01 mg L⁻¹). The maximum K⁺ concentration was noted in Sakhi Sarwar Road (85.7 mg L⁻¹), while the minimum was observed in Lundi Saidan (70 mg L⁻¹). The maximum concentration of Na⁺ was recorded in Fort Munro Road (315.53 mg L⁻¹), while the minimum was in Dara Kaha (215.7 mg L⁻¹). The maximum Cl⁻ concentration was observed in Lundi Saidan (656.89 mg L⁻¹), while the minimum was in Sakhi Sarwar Pull (280.6 mg L⁻¹). The maximum NO₃⁻ level was observed in Lundi Saidan (2.84 mg L⁻¹), while the minimum was in Fort Munro Road (1.72 mg L⁻¹). The maximum PO₄³⁻ concentration was recorded in Lundi Saidan (9.2 mg L⁻¹), while the minimum was in Sakhi Sarwar Pull (6.23 mg L⁻¹). The maximum soil saturation percentage was recorded in Dara Kaha (42%), while the minimum was in Fort Munro Road (35%).

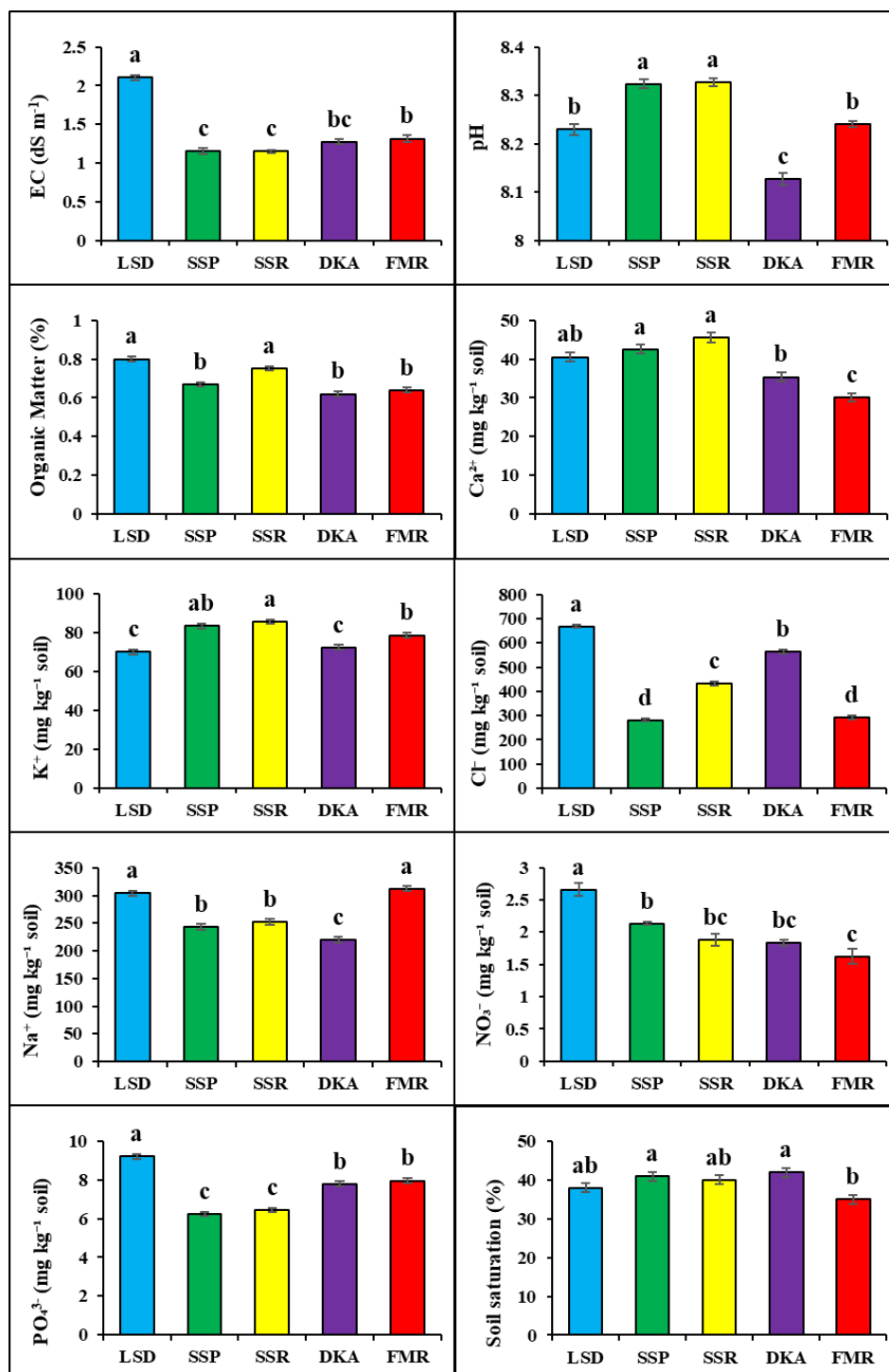


Figure 1: Physicochemical properties of rhizosphere soil (Saturated paste) collected from different habitats in the Koh-e-Suleiman region, Punjab, Pakistan. LSD: Lundi Saidan; SSP: Sakhi Sarwar Pul; SSR: Sakhi Sarwar Road; DKA: Dara Kaha; FMR: Fort Munro Road. Bars bearing different alphabets differ significantly at $p < 0.05$.

Morphological characteristics

The maximum root length was recorded in the Lundi Saidan population (6.8 cm), while the minimum was in Fort Munro Road (6.2 cm) (**Figure 2**). The maximum plant height was observed in the Lundi Saidan population (110 cm), while the minimum was in Fort Munro Road (60 cm). The leaf area was the maximum in the Lundi Saidan (6.5 mm²), while the minimum was in Fort Munro Road (3.3 mm²). The maximum number of leaves per branch was noted in the Lundi Saidan ecotype (28), while the minimum was in Fort Munro Road (13).

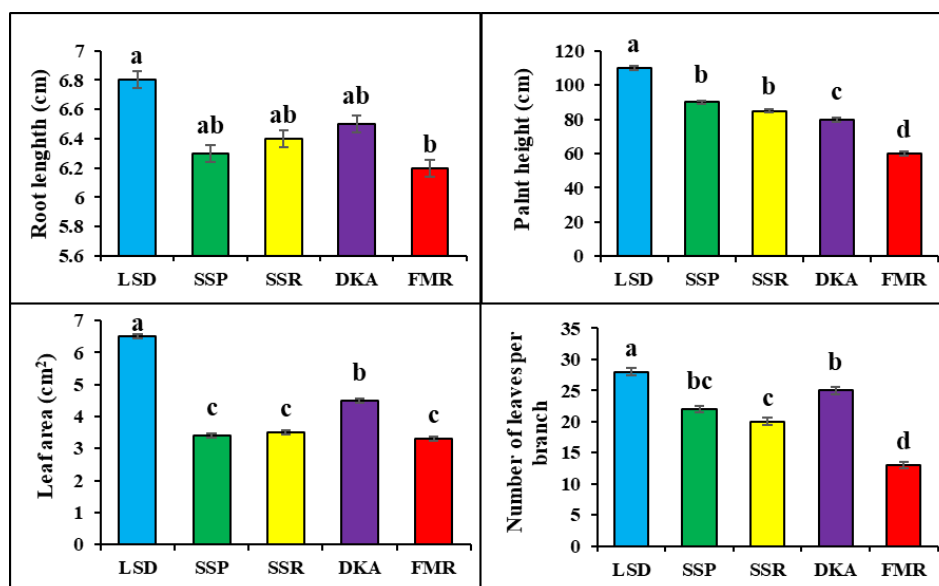


Figure 2: Morphological characteristics of different populations of *Withania coagulans* collected from different habitats in the Koh-e-Suleiman region, Punjab, Pakistan. LSD: Lundi Saidan; SSP: Sakhi Sarwar Pul; SSR: Sakhi Sarwar Road; DKA: Dara Kaha; FMR: Fort Munro Road. Bars bearing different alphabets differ significantly at $p < 0.05$.

Anatomical characteristics

Root anatomy

The maximum epiblema thickness was observed in the Sakhi Sarwar Road ecotype, while the minimum was in Sakhi Sarwar Pul (**Figures 3 and 5**). The maximum cortical thickness was observed in the Sakhi Sarwar Road population, while the minimum was observed in Lundi Saidan. The maximum phloem thickness was observed in Sakhi Sarwar Pul, while the minimum was in Fort Munro Road. The maximum metaxylem area was observed in the Lundi Saidan ecotype, while the minimum was in Sakhi Sarwar Road. The maximum stellar region area was recorded in Sakhi Sarwar Pul, while the minimum was in Sakhi Sarwar Road. The maximum endodermal thickness was recorded in Dara Kaha, while the minimum was in Sakhi Sarwar Road. The maximum root radius was observed in Fort Munro Road, while the minimum was in the Sakhi Sarwar Road population.

Stem anatomy

The maximum epidermal thickness was observed in the Fort Munro Road ecotype, while the minimum was in Sakhi Sarwar Road (**Figures 3 and 6**). The maximum cortical thickness was noted in Dara Kaha, while the minimum was in Fort Munro Road. The maximum phloem thickness was documented in Sakhi Sarwar Pul, while the minimum was in Fort Munro Road. The maximum metaxylem area was found in Fort Munro Road, while the minimum was in Dara Kaha. The maximum pith area was observed in Dara Kaha, while the minimum was in Lundi Saidan. The maximum pith cell area was observed in Dara Kaha, while the minimum was in Lundi Saidan. The Dara Kaha population displayed the maximum stem radius, while the Lundi Saidan ecotype had the minimum stem radius.

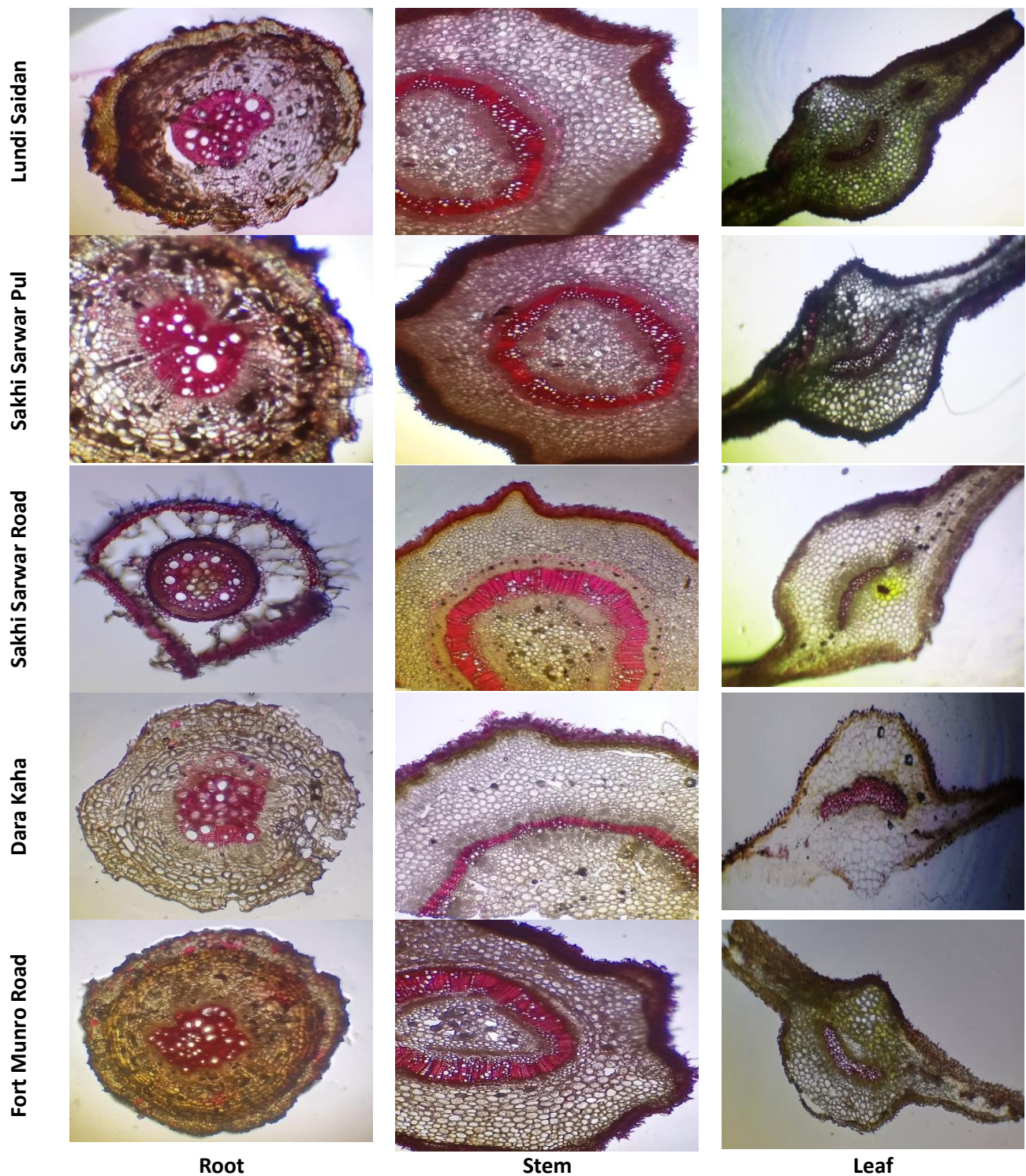


Figure 3: Transverse sections of root, stem, and leaf of different populations of *Withania coagulans* collected from various regions of Koh-e-Suleiman, Punjab, Pakistan

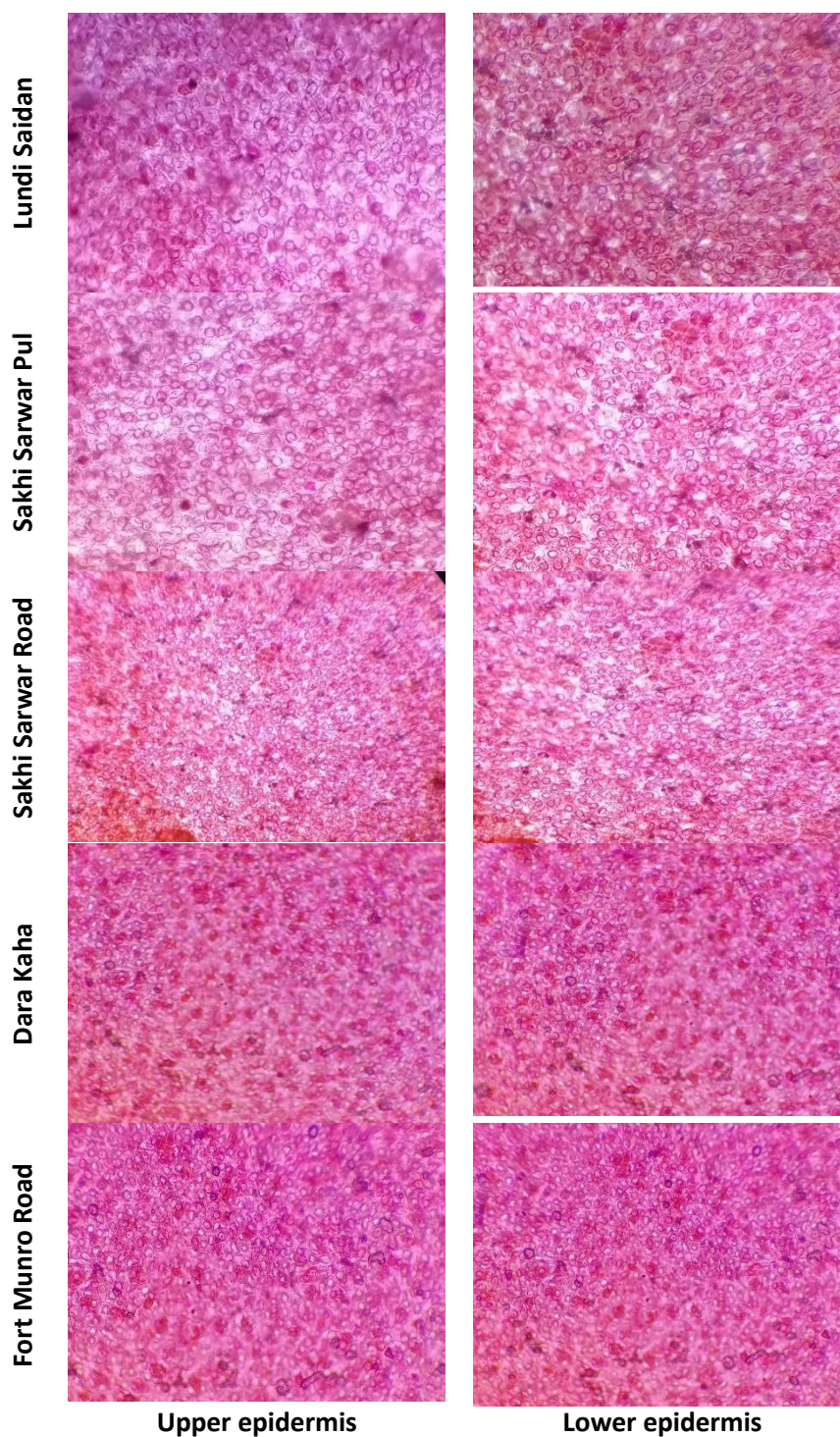


Figure 4: Leaf epidermal view of different populations of *Withania coagulans* collected from various regions of Koh-e-Suleiman, Punjab, Pakistan.

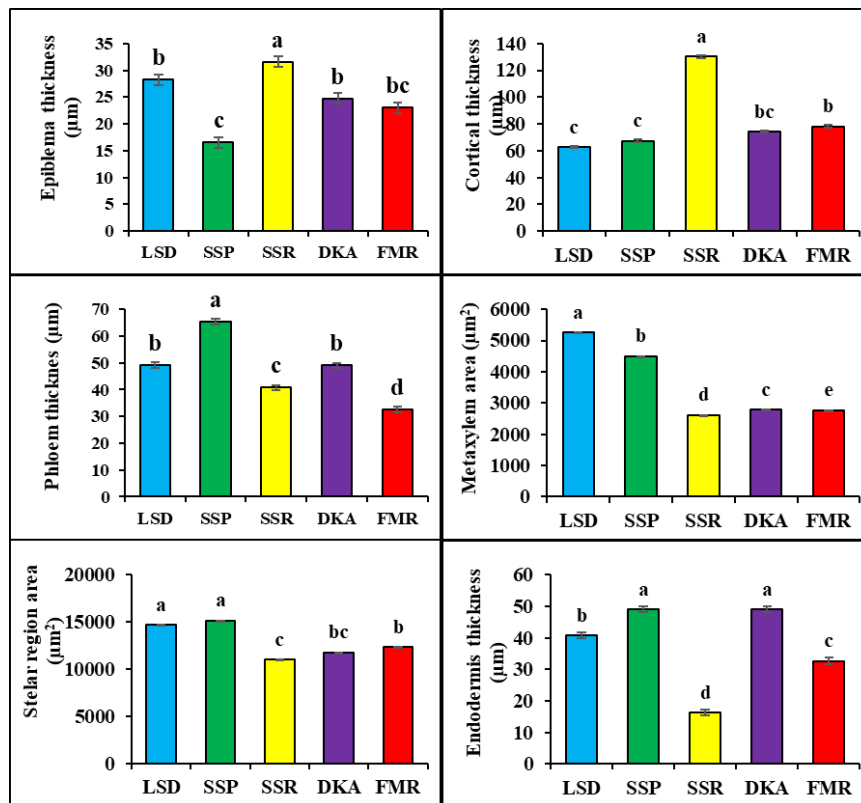


Figure 5: Root anatomical characteristics of different populations of *Withania coagulans* collected from different habitats in the Koh-e-Suleiman region, Punjab, Pakistan. LSD: Lundi Saidan; SSP: Sakhi Sarwar Pul; SSR: Sakhi Sarwar Road; DKA: Dara Kaha; FMR: Fort Munro Road. Bars bearing different alphabets differ significantly at $p < 0.05$.

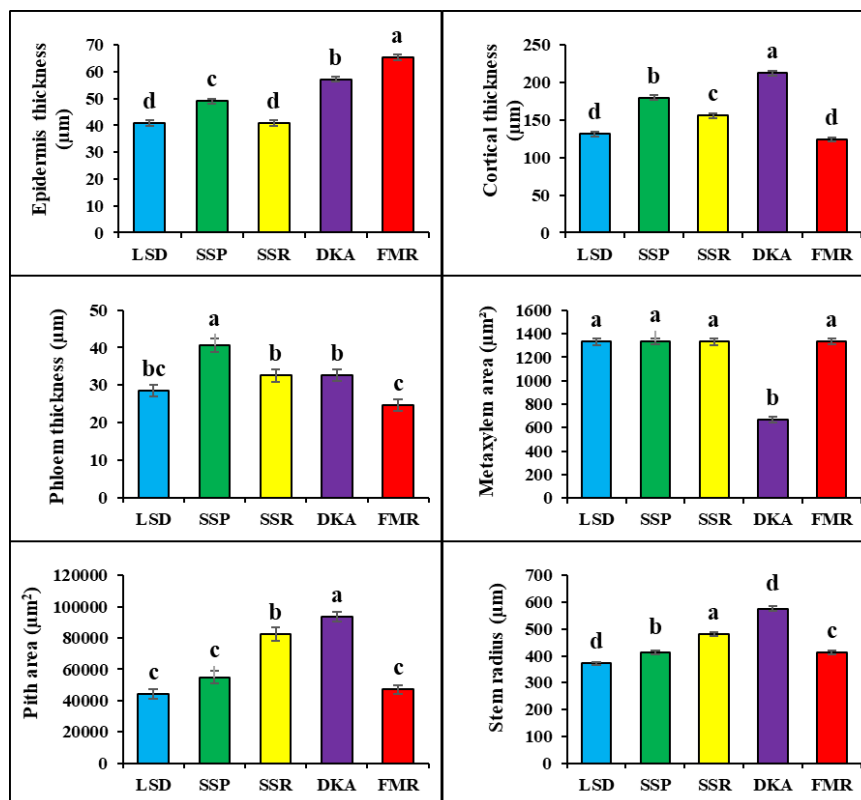


Figure 6: Stem anatomical characteristics of different populations of *Withania coagulans* collected from different habitats in the Koh-e-Suleiman region, Punjab, Pakistan. LSD: Lundi Saidan; SSP: Sakhi Sarwar Pul; SSR: Sakhi Sarwar Road; DKA: Dara Kaha; FMR: Fort Munro Road. Bars bearing different alphabets differ significantly at $p < 0.05$.

Leaf anatomy

The maximum upper epidermal thickness was observed in the Sakhi Sarwar Pul population, whereas the minimum was recorded in Fort Munro Road (Figures 4 and 7). The Sakhi Sarwar Pul population showed the maximum lower epidermal thickness, while the Fort Munro Road ecotype displayed the minimum epidermal thickness. The maximum midrib thickness was observed in Sakhi Sarwar Pul, while the minimum was in Fort Munro Road. The Sakhi Sarwar Pul ecotype displayed the maximum cortical region thickness, whereas the Lundi Saidan showed the minimum cortical region thickness. The maximum vascular bundle area was observed in Lundi Saidan, while the minimum was in Sakhi Sarwar Road. The maximum metaxylem area was the maximum in Lundi Saidan, while the minimum was recorded in Fort Munro Road. The Lundi Saidan population showed the maximum lamina thickness, whereas the Dara Kaha ecotype showed the minimum lamina thickness. The maximum mesophyll thickness was observed in Dara Kaha, while the minimum was in Fort Munro Road. The maximum number of stomata was documented in Lundi Saidan, while the minimum was in Dara Kaha. The Dara Kaha ecotype displayed the maximum stomatal area, whereas the Sakhi Sarwar Pul ecotype displayed the minimum stomatal area.

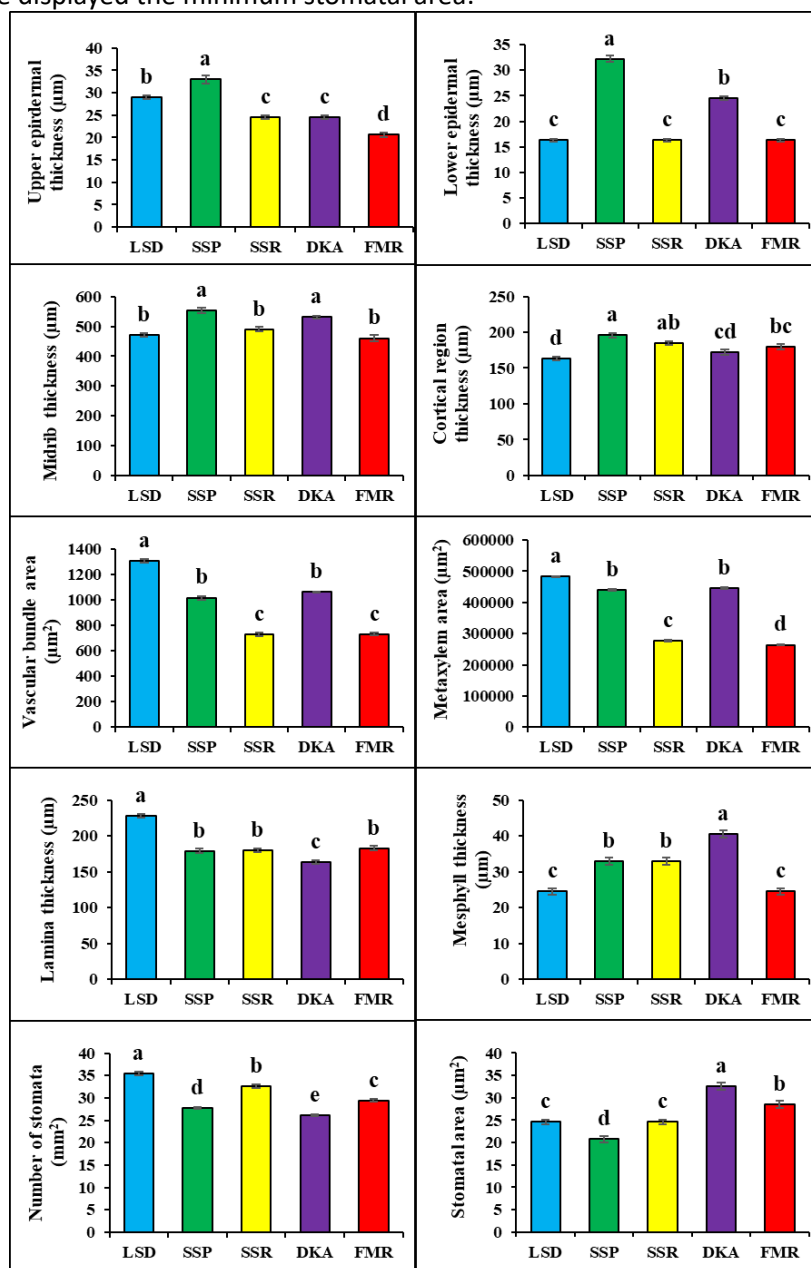


Figure 7: Leaf anatomical characteristics of different populations of *Withania coagulans* collected from different habitats in the Koh-e-Suleiman region, Punjab, Pakistan. LSD: Lundi Saidan; SSP: Sakhi Sarwar Pul; SSR: Sakhi Sarwar Road; DKA: Dara Kaha; FMR: Fort Munro Road. Bars bearing different alphabets differ significantly at $p < 0.05$.

Discussion

Generally, plants growing in heterogeneous environmental conditions respond to climatic and edaphic stresses through the manifestation of morphological and anatomical plasticity. The unpredictable changes in plants in response to multiple stresses tend to affect plant growth and survival as environmental factors like salinity, drought, temperature extremes, and elevation are not predictable but alter very fast (Niu et al., 2014; Jing et al., 2024). The vulnerability of high-altitude plants to climatic change compared to low-altitude populations is usually higher because of low temperatures and less availability of CO₂ in the atmosphere (Körner, 2002; Zhang et al., 2024).

The research presented in this study compared morphological and anatomical differences among the populations of *Withania coagulans* collected from different habitats within the Koh-e-Suleiman region (Punjab, Pakistan) and their survival in adverse environmental and soil conditions. The site-specific variation of morphological features seemed to be evident. The Lundi Saidan population ranked the highest in root length, plant height, leaf area, and the number of leaves per branch, whereas these characteristics were the minimum for the Fort Munro Road ecotype. The increased soil salinity and ion concentration, especially the high soil electrical conductivity (ECe) and Cl⁻ levels in the Lundi Saidan ecotype, might have increased uptake of water and nutrients by the roots, since the root length was higher in this population, as compared to the other populations. Both higher plant height and number of leaves could translate to increased biomass allocation and potential growth in the given environmental conditions (Poorter et al., 2012; Miao et al., 2024). Alternatively, the lower plant height, leaf area, and root length in Fort Munro Road might be explained by the high elevation and low temperature, which might limit the growth of cells and vegetative growth. A decrease in leaf area is usually linked to stress avoidance strategies, which restrict the amount of water evaporated through transpiration in colder or drier environments (Peguero-Pina et al., 2020). The morphological patterns recorded in this study indicate that *W. coagulans* has high levels of phenotypic plasticity in response to environmental gradients in the ecosystem.

Root anatomical characteristics also favored adaptive differentiation between the populations. The Sakhi Sarwar Road ecotype had the highest values of epiblema and cortical thickness, which reflects improved protection and storage capacity of the ecotype at moisture-limited or saline conditions. An increased cortex has been reported to improve the level of water storage and aid in osmotic adjustment during physiological drought (Ahmad et al., 2018; Zahedi et al., 2025). The highest metaxylem area in Lundi Saidan indicates high hydraulic conductivity, which promotes effective transport of water during saline stress (Chattha et al., 2024). On the same note, the optimum thickness of the phloem in Sakhi Sarwar Pul could be an empowering force in the process of translocation of photoassimilates, which is vital in maintaining growth in cases of stress (Shakya and Lal, 2018; Li et al., 2026).

The maximum endodermal thickness measured in Dara Kaha seems to be an adaptive barrier to control the inflow of ions and reduce the loss of water. It has been found that thickened endodermal and exodermal layers have protective functions in saline conditions by limiting the excessive salt penetration into the vascular tissues (Reinhardt and Rost, 1995; Robbins et al., 2014). The fact that the root radius was the largest in the Fort Munro Road population indicates that the structure is reinforced and can therefore resist mechanical stress and increase capacity to store water at elevated levels (Galpathage, 2017).

There was a significant variation in stem anatomical characteristics across different populations of *Withania coagulans*. The minimum epidermal thickness in Lundi Saidan can be explained by the fact that salinity has the capacity to decrease the epidermal cell size and thickness (Hameed et al., 2010; Zörb et al., 2015). Conversely, the maximum cortical thickness of the Dara Kaha population signifies formation of succulence, a typical adaptive trait in a water-inadequate or salty environment that increases internal storage of water (Herbst, 2001; Wasim and Naz, 2020). The answer to this is the maximum phloem thickness of the Sakhi Sarwar Pul ecotype that facilitates increased transport of assimilates, and there are site-specific hydraulic accommodations indicated by changes in the metaxylem area (Strock et al., 2021). The Dara Kaha population pith area and stem radius were the largest, and probably they led to higher water storage and mechanical support, less risk of dehydration, and higher stress tolerance (Oliver et al., 2020).

Anatomical patterns of leaves showed high adaptive patterns in the *W. coagulans* populations. The decreased upper and lower epidermal thickness and midrib thickness in the Sakhi Sarwar Pul population show its vulnerability against water evaporation. Xeromorphological features such as thick epidermal layers and development of the cuticle can effectively reduce the transpiration during

drought stress and salinity stress (Yavas et al., 2024; Zahedi et al., 2025).

Moreover, the largest vascular bundles and metaxylem area in the Lundi Saidan ecotype indicate that water and nutrient conduction could be expected under high salinity, and these guarantees continued physiological activity (Marusig and Tombesi, 2020). Furthermore, the highest stomata count in Lundi Saidan indicates a balance between water and gas exchange. Although higher stomatal density can lead to higher photosynthetic efficiency, stomatal size and distribution control can help plants to reduce unwarranted loss of transpiration during stress (Hasanuzzaman et al., 2023).

Conclusion

Environmental variation due to elevation has a strong influence on the morphological and anatomical characters of *Withania coagulans*, particularly in the highlands of Koh-e-Suleiman. The variation in plant height, root length, and leaf area is an indication of adaptive growth to local climatic and edaphic conditions. Root, stem, and leaf structural adaptations, especially those in vascular development, cortical thickening, and epidermal thickness, facilitate effective water transport, water storage, and transpiration regulation in stress-prone environments. In general, the identified trait plasticity demonstrates the adaptability of *W. coagulans* and facilitates its preservation and localized application in mountainous and arid areas.

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

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Contribution of authors

Research supervision: SMRS. Conceptualization and designing the study: MJ, ZA. Conduction of experiment: MF, AM. Resource availability: MU, HF, MI. Moderation of laboratory activities: ZA, MJ. Instrumentation and analysis: BA, SFN, SM. Preparation of initial draft: SMRS, M. 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.

Authors' consent

All authors have critically read this manuscript and agreed to publish in IJAEB.

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