



RESEARCH ARTICLE

Ecological-anatomical adaptations of *Mentha longifolia* under *in situ* and *ex situ* conditions

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Abstract

This study aims to determine the effects of environmental factors across different ecosystems on the anatomy of the medicinally important species *Mentha longifolia* L. and to reveal its adaptation mechanisms. Comparative analyses were performed using anatomical, microscopic, histochemical and biometric methods to clarify the extent and nature of anatomical variability in ecotypes of the species, thereby exploring their potential for environmental adaptation. Anatomical sections of the species were stained using histological reagents and permanent slides were prepared for subsequent analysis. This study represents the first comparative analysis of the ecological-anatomical characteristics of *M. longifolia* under *in situ* and *ex situ* conditions. Furthermore, statistical analysis of micrometric indicators confirmed the species' climatic resilience and adaptive responses to stress. In the *in situ* ecotype, parenchymatic excretion, an active "punctate-porous" cellular structure in the rhizome and well-developed aerenchyma (in rhizome cortex - *in situ*: $51.51 \pm 4.955 \mu\text{m}$; *ex situ*: $43.29 \pm 4.014 \mu\text{m}$) were identified. In *ex situ* specimens, parenchyma cell size differences were statistically significant (e.g., in the leaf - *in situ*: $31.52 \pm 2.279 \mu\text{m}$; *ex situ*: $37.51 \pm 2.465 \mu\text{m}$). Additionally, variations were observed in the xylem lumen diameter (e.g., in the stem - *in situ*: $23.54 \pm 1.664 \mu\text{m}$; *ex situ*: $29.31 \pm 2.252 \mu\text{m}$). The structural adaptations revealed through comparative ecological-anatomical studies represent evolutionary advancements in plant anatomy and possess substantial scientific and practical relevance. This comprehensive research, systematically conducted for the first time on Azerbaijan's flora, confirms the ecological plasticity of the species.

Keywords: capitate and tectorial trichomes; dorsoventral leaf; epistoma; exodermis; parenchymatic excretion; punctate-porous structure

Introduction

In recent decades, climate change, anthropogenic impacts and ecosystem degradation have led to the reduction of the natural distribution areas of many plant species, as well as to significant alterations in their morphological, anatomical and physiological structures. Under such conditions, the study of structural adaptation mechanisms in plants has become one of the central research directions of ecological anatomy. The investigation of anatomical and phytochemical adaptation mechanisms of medicinally important species under the influence of ecological factors in both *in situ* and *ex situ* conditions is of great scientific and practical significance - not only for elucidating their systematic and physiological characteristics, but also for determining their anatomical resilience potential to environmental stressors. This approach allows for the assessment of the ecological plasticity level of medicinal plants and the identification of factors influencing the quality of medicinal raw materials.

In recent years, comparative studies on the ecological-anatomical responses of plants across different ecotopes have become increasingly widespread at the international level (1–5). The author has also examined the effects of ecological factors on tissue structure, parenchyma, mechanical and secretory tissue development dynamics in several medicinal plant species belonging to the flora of Azerbaijan (6–9). The results of these investigations

contribute to explaining the morpho-functional variability of plant organs in response to ecotopic conditions and to preserving a resilient gene pool capable of withstanding environmental change.

Mentha longifolia (Lamiaceae) is a perennial medicinal plant with hygrophytic characteristics, widely distributed in the mountainous and foothill regions of Azerbaijan. Its ability to propagate vegetatively through rhizomes and its broad ecological amplitude make it a suitable model species for studying adaptation potential across different ecosystems. The anatomical structure of its leaf, petiole, stem, root and rhizome organs exhibits a sensitive response to environmental conditions, providing an opportunity to evaluate the plants' level of structural plasticity. The stem of the plant is quadrangular and the short-petioled leaves are oppositely arranged. Leaves are lanceolate, tapering toward the tip (10). Near the apex of the plant, sympodial branches form, culminating in inflorescences.

It is well known that species belonging to the genus *Mentha* are rich in essential oils and biologically active compounds (11–13). However, information regarding their anatomical variability and structural adaptation mechanisms in response to environmental conditions remains very limited. Although studies conducted in various countries have investigated the adaptive characteristics of other plant species cultivated under *ex situ* conditions, the comparative analysis of micromorphological and metabolomic

adaptations in the vegetative organs of *M. longifolia* across different ecosystems (mid-mountain and low-altitude zones) has not been carried out to date (14–17). The present study, for the first time, aims to analyse the characteristic features of anatomical adaptation in *M. longifolia* under *in situ* and *ex situ* ecological conditions, as well as to assess the influence of various ecological factors on the structural responses of plant tissues. These findings not only contribute new information to the fundamental field of ecological anatomy but also provide valuable insights into the evaluation of ecological adaptation in medicinal plants in terms of bioconservation and resource management.

Materials and Methods

Material collection

Mentha longifolia specimens were originally collected in May 2021 from the Kalbajar region (40°07'08"N, 46°03'39" E) and cultivated under *ex situ* conditions as a container culture in the Bala Bagman area of Ganja city (40°39'57" N, 46°20'36" E). After one year of container growth, the plants were transplanted into open soil conditions and allowed to grow naturally without any artificial intervention. The altitude and climatic factors of the study areas were presented and their ecological effects on the investigated species were clarified (Fig. 1–3). Field sites in Kalbajar were characterised by grassy mountain-meadow vegetation on brown to dark-brown mountain forest soils, while *ex situ* collections in Ganja were associated with gray-brown soils, providing a context for interpreting anatomical variation in relation to soil type and moisture conditions (18). The collection of plant materials was carried out three years after introduction and spontaneous cultivation for the *ex situ* samples, while the *in situ* specimens were collected naturally from the mountainous ecosystem. In both ecotypes, sampling was performed during the vegetation period, specifically at the flowering and intensive growth stages, allowing for a more precise evaluation of the relationship between anatomical parameters and environmental conditions. To ensure the inclusion of representative plant specimens, material collection was conducted between 2021 and 2024.

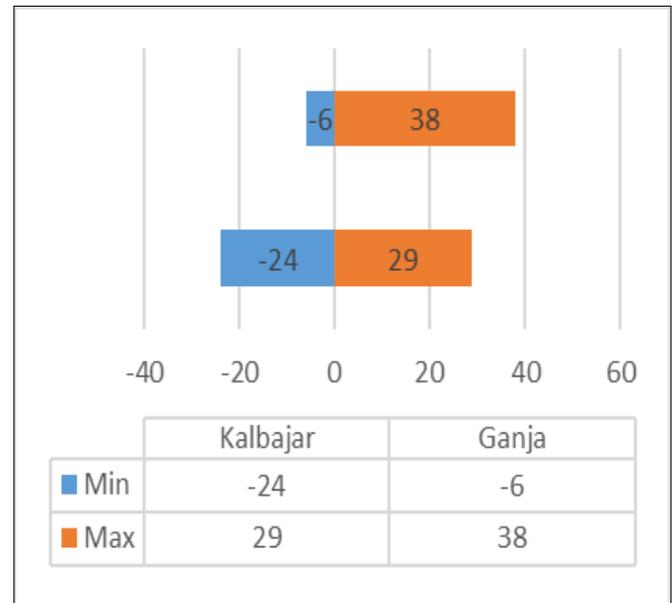


Fig. 2. Temperature variation (Min-Max) across sites (°C).

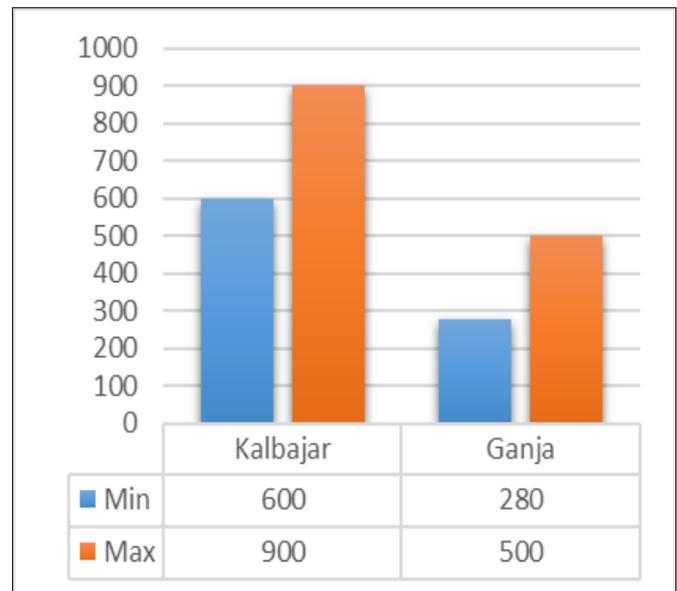


Fig. 3. Annual minimum and maximum precipitation (mm).

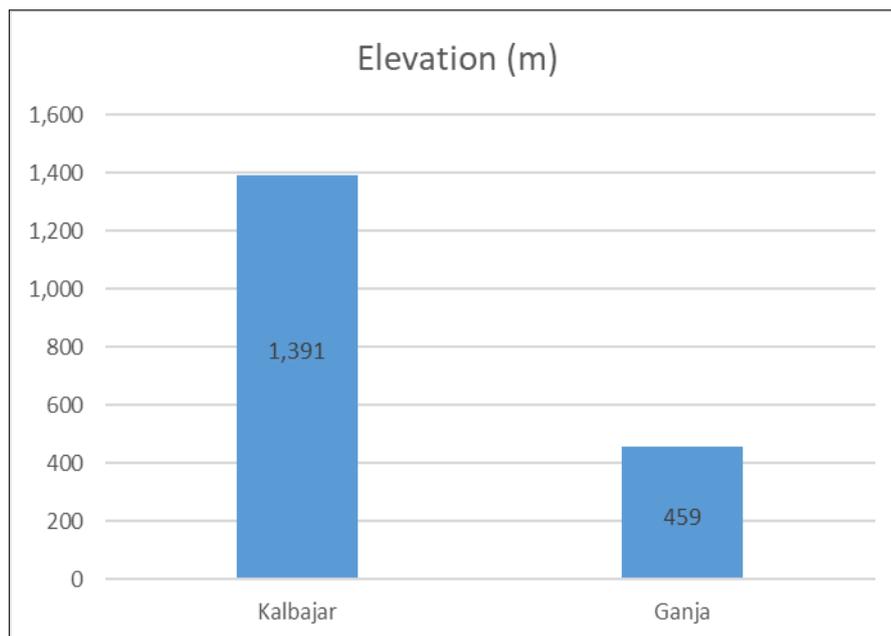


Fig. 1. The elevation of the research areas (m).

Material processing

The collected plant specimens were placed in fixatives and subsequently, anatomical sections were prepared from the fixed material using a microtome (Radical, RMT-5, India). During this process, paraffin (BW Blended Waxes, Inc., US) was used as both an embedding and cutting medium. Section thickness was calibrated using the microtomes' micrometric adjustment screw and measured in microns. Sections were cut at thicknesses ranging from 7 to 8 μm .

Following sectioning, differential histochemical staining was applied using specific reagents such as safranin O, fast green, Sudan III, toluidine blue, phloroglucinol-HCl and methylene blue (KimyaLab, Turkey). The staining process was performed stepwise using a decolourisation method to achieve selective tissue colouration (19-22). This approach enabled precise differentiation of the ecological-anatomical structures of *M. longifolia* under both *ex situ* and *in situ* conditions. Permanent slides were prepared by mounting stained sections in Canada balsam (Innovating Science, US) on microscope slides, which were covered with a cover slip. The slides were incubated in a controlled environment (20–25 °C) until the mounting medium completely dried. These permanent transverse sections were then subjected to microscopic analysis.

Microscopic studies

Microscopic observations were carried out at the Biology department laboratory of Azerbaijan State Agricultural University using a "Carl Zeiss, Axio Imager A2" microscope (Zeiss, Germany) equipped with LED illumination and objective lenses with minimal aberration (5 \times , 10 \times , 20 \times , 40 \times , 100 \times). In addition, an LCD Digital Microscope (NLCD-307B, Wincom Company Ltd., China) was employed during earlier stages to monitor the quality of sectioning and staining before slide preparation. Final analyses, image capture and quantitative measurements were conducted using the Carl Zeiss Axio Imager A2 system. Observations at 100 \times magnification were performed with immersion oil (RMY, US), enhancing optical resolution and contrast of the microscopic images. Stereomicroscopes (Zeiss Stemi 508, ZEISS, Germany and YK-SM067B2, Wincom Company Ltd., China) were also used for macroscopic examination of plant tissues.

Biometric methods

To verify the accuracy of micrometric data obtained via microscope analysis, both eyepiece and stage micrometres (Muhva, China) were employed. Initially, calibration of the eyepiece micrometre was performed using the stage micrometre, after which measurements were made based on micrometric scales. Additionally, macroscopic dimensions of plant organs were recorded using a digital micrometre (Jiavarry, China). All measurements were annotated directly on photomicrographs (23).

Herbarium preparation

Herbarium specimens prepared from the medicinally valuable *M. longifolia* served as reference material not only for detailed ecological and anatomical assessments but also for pharmacognostic and phytotherapeutic evaluations. Specimens from both *in situ* and *ex situ* conditions were incorporated into the herbarium collection of the Biology Department at Azerbaijan State Agricultural University, named after Academician Valida Tutayuy. These specimens are preserved as part of a systematically catalogued botanical collection available for research, educational and reference purposes (Voucher Numbers: ASAU-ML-2021-IS6 and ASAU-ML-2024-EX7).

Statistical method

Samples of *M. longifolia* from two ecologically distinct regions of Azerbaijan were statistically analysed based on various anatomical parameters. From each location, 8–12 different individual plants were selected and vegetative organs were sampled for analysis. For each organ, 10–15 transverse sections were prepared and examined microscopically. Multiple parameters were measured and all data were analysed using the Jamovi statistical software (version 2.6.26, University of Sydney, Australia). Results were presented as mean and standard deviation (SD). The Shapiro-Wilk test was applied to assess the normal distribution of data ($W > 0.05, p > 0.05$). Subsequently, an independent samples t-test was used to determine the significance of differences between the ecotypes. The results ($p < 0.05$) demonstrated that the structural characteristics of the plant varied significantly between *in situ* and *ex situ* environments.

Results and Discussion

Leaf

The leaf of *M. longifolia* exhibits a dorsoventral anatomical structure. In transverse sections, a prominent central vascular bundle is observed. In the *in situ* plants, the central vascular system is composed of xylem elements with more heavily lignified walls and the vascular tissues are arranged in a more orderly manner compared to the *ex situ* samples. The sclerenchyma tissue surrounding the central conducting system is relatively less developed in *ex situ* leaves. In the leaves of *ex situ* plants, the parenchymal tissue is more developed and occupies an expanded area extending from the sides of the central vascular bundle towards the subepidermal regions (24). The parenchymal cells are noticeably larger in the *ex situ* samples (Table 1, Fig. 4). Additionally, the number of xylem rays and vessels is slightly higher in these specimens. The central vascular bundle is surrounded by parenchymal tissue, whose cell walls appear more thickened in *in situ* samples (Table 2). This thickening is particularly evident in the subepidermal regions, especially in the collenchyma cells. In *ex situ* samples, a well-structured collenchyma tissue is observed in the subepidermal layers.

The mesophyll of *M. longifolia* is differentiated into palisade and spongy parenchyma. In the *in situ* specimens, the palisade parenchyma consists of a single layer of elongated cells. In the *ex situ* specimens, this tissue is also predominantly single-layered; however, in certain regions - particularly near the lateral vascular bundles - a weakly developed second layer of cells can be observed. The spongy parenchyma in the *in situ* samples generally appears as a compact tissue composed of three cell layers, whereas in the *ex situ* specimens it consists of three to four layers (Fig. 5A & B). The leaf surface is covered with both tectorial and conical trichomes and also contains very small capitate trichomes (Table 3 & 4). These capitate trichomes are capable of synthesising essential oils and various secondary metabolites. The conical trichomes present in the plant are composed of a single cell. In the leaves of the plant grown under *ex situ* conditions, the density of trichomes was reduced, whereas their basal thickness was increased.

Petiole

The petiole of *M. longifolia* displays a crescent-like shape and is relatively larger in *ex situ* specimens. In the *ex situ* samples, the centrally located narrow and elongated vascular bundle is

Table 1. Leaf tissue measurements and statistical comparison of *in situ* and *ex situ* individuals of the species *Mentha longifolia*

Indicators	Areas	Mean (μm)	SD (μm)	Shapiro-Wilk		Independent Samples T-Test
				W	p	p
The height of the adaxial epidermis cells	<i>In situ</i>	19.63	0.788	0.944	0.603	<0.001
	<i>Ex situ</i>	23.46	0.795	0.960	0.784	
Diameter of the parenchyma cells	<i>In situ</i>	31.52	2.279	0.966	0.848	<0.001
	<i>Ex situ</i>	37.51	2.465	0.954	0.715	
The height of the central vascular bundle	<i>In situ</i>	123.77	5.483	0.955	0.723	0.010
	<i>Ex situ</i>	130.64	5.245	0.934	0.489	
Diameter of the xylem lumen	<i>In situ</i>	11.74	0.889	0.946	0.623	<0.001
	<i>Ex situ</i>	22.68	1.521	0.937	0.522	

SD - standard deviation. Shapiro-Wilk test confirmed normal distribution ($W > 0.05$, $p > 0.05$); t-test indicated a significant difference between groups ($p < 0.05$).

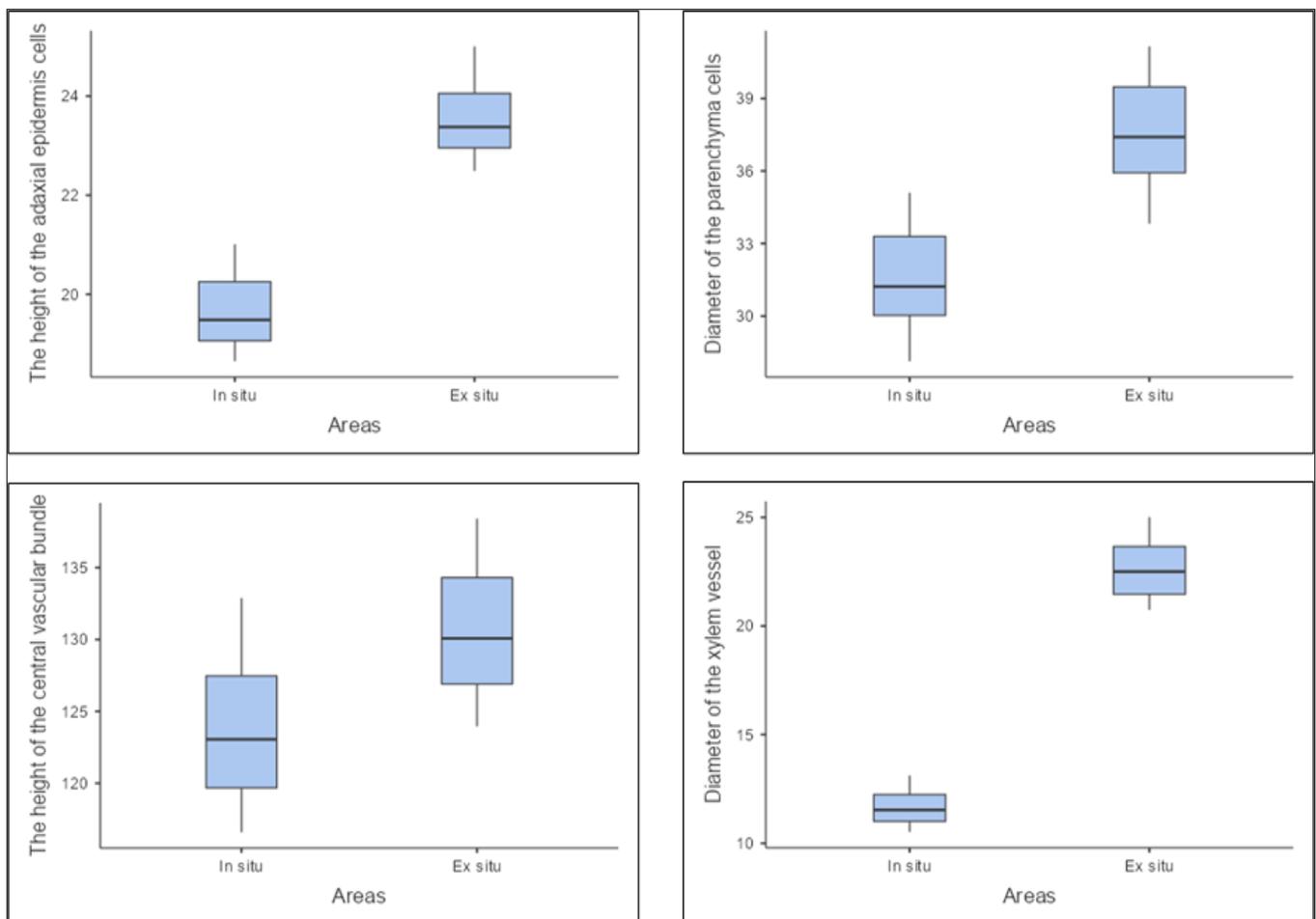
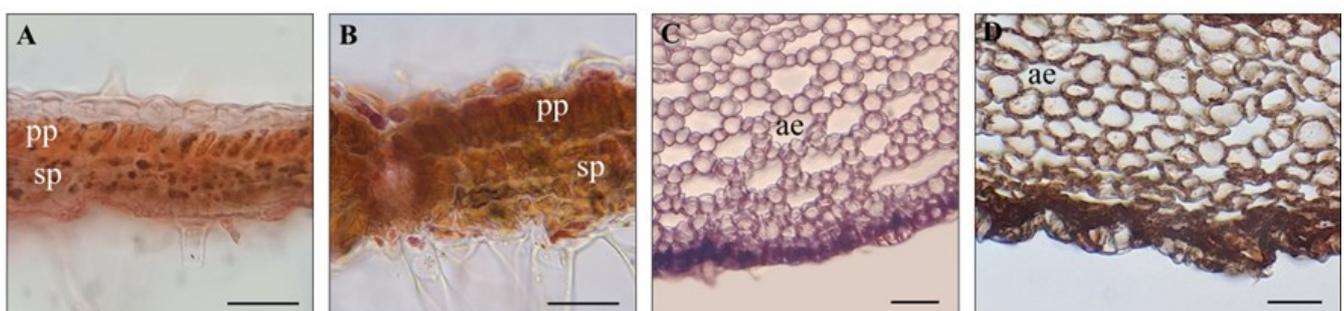
**Fig. 4.** Comparative box plots of species *Mentha longifolia* leaf measurements from *in situ* and *ex situ* samples.**Fig. 5.** *Mentha longifolia*. Leaf mesophyll structure A. *In situ*, B. *ex situ* and aerenchyma formed in the cortex of the rhizome, C. *In situ*, D. *ex situ*. pp-palisade parenchyma; sp- spongy parenchyma; ae-aerenchyma; scale bar: 50 μm .

Table 2. Microscopic analysis of anatomical structure differences in leaf samples of *Mentha longifolia* collected from the *in situ* and *ex situ* conditions

Description of anatomical features	<i>In situ</i>	<i>Ex situ</i>
Transverse section of the leaf, co.tr - conical trichome, ca.tr - capitate trichome, te.tr - tectorial trichome (scale bar: 500 μ m)		
Midrib region, pa - parenchyma (scale bar: 300 μ m)		
Structure of the vascular tissue, xy - xylem, ph - phloem (scale bar: 40 μ m)		
Collenchyma tissue on the abaxial side of the leaf, cl - collenchyma (scale bar: 100 μ m)		
Tectorial trichomes (scale bar: 100 μ m)		

"8 μ m" shown on the first image indicates the section thickness.

Table 3. Trichomes on different organs of the *in situ* specimen of the species *Mentha longifolia*

Capitate trichome on the leaf (scale bar: 30 μm)



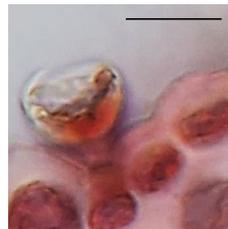
Capitate trichome on the petiole (scale bar: 30 μm)



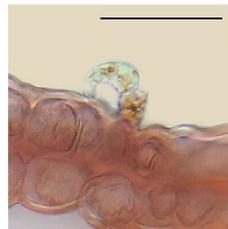
Capitate trichome on the stem (scale bar: 30 μm)



Capitate trichome on the stem (scale bar: 10 μm)



Capitate trichome on the stem (scale bar: 30 μm)

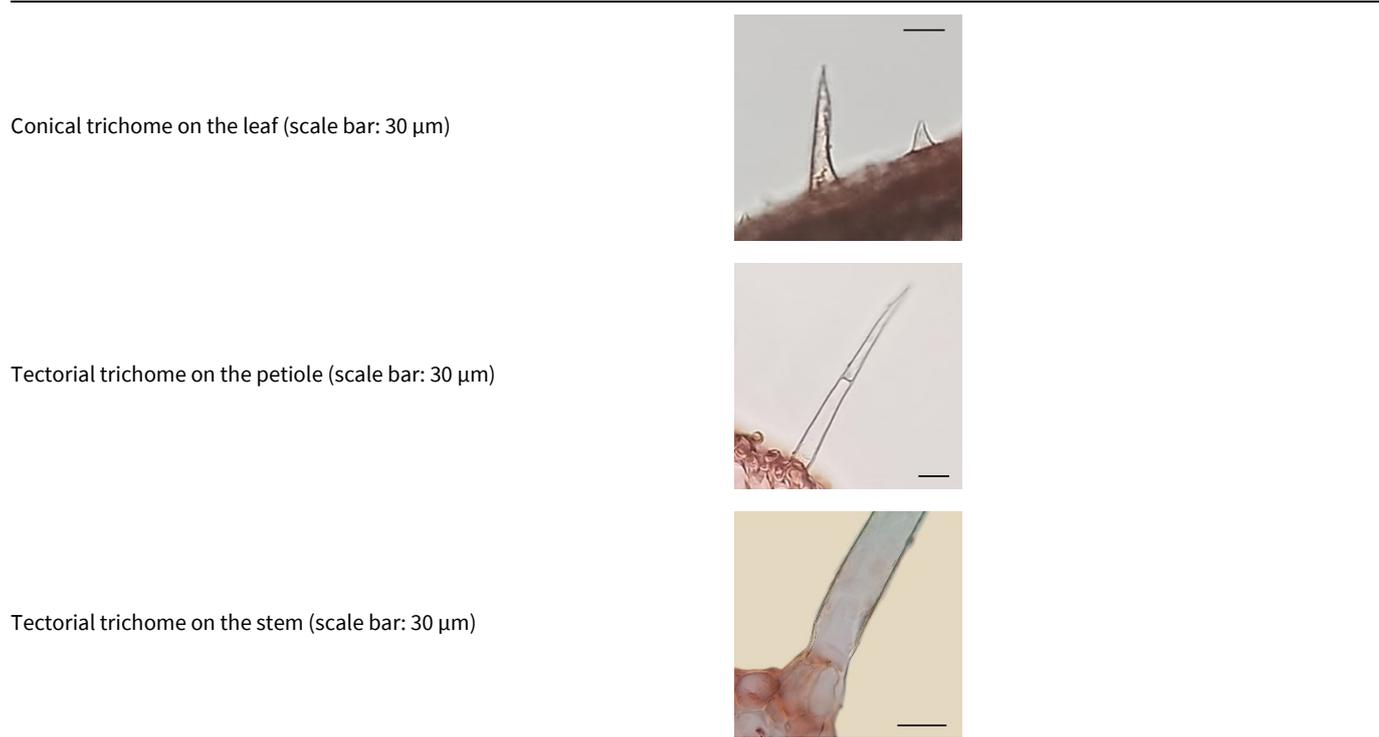


Tectorial trichome containing accumulated substances on the stem (scale bar: 30 μm)



Conical trichome on the leaf (scale bar: 30 μm)



Table 4. Trichomes on different organs of the *ex situ* specimen of the species *Mentha longifolia*

accompanied by smaller lateral bundles on either side (25). Upon examining the developmental features, it is evident that the vascular bundles in the *in situ* plants are more robustly developed. The xylem elements are more numerous and larger in diameter compared to the *ex situ* samples. Furthermore, the phloem and associated mechanical tissues are better organised, with the phloem encircling the xylem dorsally. In *in situ* petioles, the cell walls of both the phloem and the surrounding mechanical tissues exhibit more pronounced thickening than those in *ex situ* samples. Additionally, small-sized, substance-rich cells are located near the vascular tissues, particularly surrounding the xylem, which contribute to the darker appearance of this region in *in situ* samples (26).

The parenchymal cells filling the internal cavity of the petiole are significantly larger in the *ex situ* samples (Table 5, Fig. 6). These cells also display slight pigmentation of the cell walls. Collenchyma tissue is observed particularly in the lower subepidermal regions of the petiole and is more developed in the *in situ* samples. In these samples, the collenchyma consists of multiple layers, with a higher

degree of cell wall thickening (Table 6). Furthermore, microscopic analysis of the leaf petiole epidermis reveals the accumulation of constitutional substances, which are more prominent in the *in situ* plants compared to the *ex situ* ones.

Stem

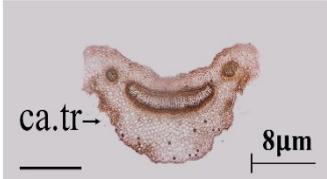
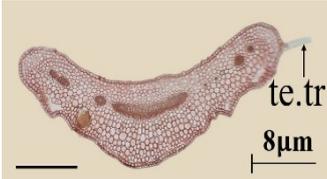
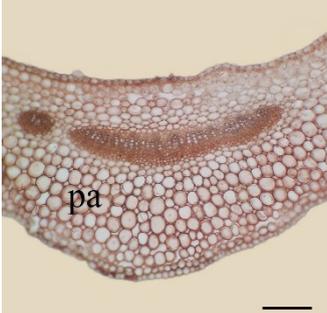
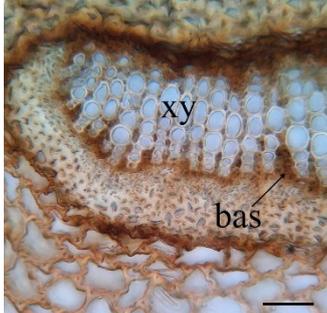
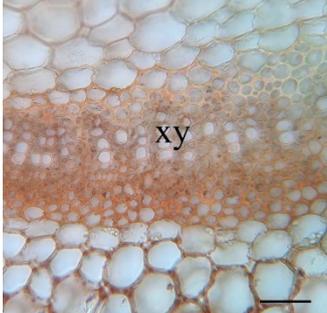
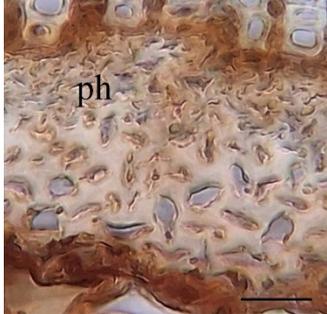
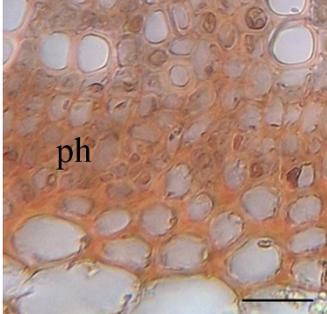
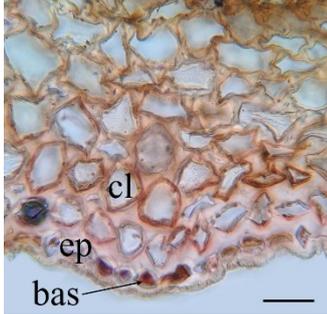
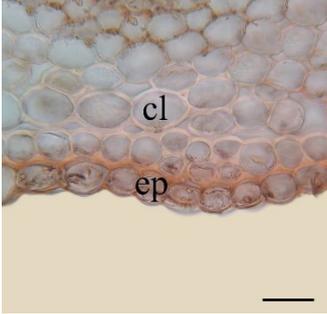
In transverse sections of the stem of *M. longifolia*, the *ex situ* samples exhibit a more voluminous structure due to the greater abundance of pith parenchyma. The pith cells are also noticeably larger in these samples. Microscopic analysis revealed a few idioblast-shaped cells containing green substances dispersed within the pith parenchyma. The vascular bundles in the *ex situ* stems are more prominently developed, with a higher number of xylem vessels. In the *in situ* samples, the phloem elements of the bundles are adjacent to cortical parenchyma, which is considerably thicker than that observed in *ex situ* stems (Fig. 7). Additionally, the cortex in the *in situ* samples exhibits numerous small, elongated aerenchymatous spaces (Table 7).

Table 5. Petiole tissue measurements and statistical comparison of *in situ* and *ex situ* individuals of species *Mentha longifolia*

Indicators	Areas	Mean (μm)	SD (μm)	Shapiro-Wilk		Independent Samples T-Test
				W	p	p
The height of the epidermis cells	<i>In situ</i>	30.58	1.670	0.977	0.945	0.012
	<i>Ex situ</i>	32.41	1.202	0.931	0.459	
The thickness of the outer walls of the epidermal cells	<i>In situ</i>	9.58	0.540	0.972	0.906	<0.001
	<i>Ex situ</i>	3.90	0.375	0.971	0.904	
Diameter of the parenchyma cells	<i>In situ</i>	42.76	3.701	0.963	0.818	<0.001
	<i>Ex situ</i>	70.86	4.402	0.986	0.989	
The height of the central bundle	<i>In situ</i>	236.23	5.852	0.987	0.992	<0.001
	<i>Ex situ</i>	147.29	4.902	0.982	0.974	
Diameter of the xylem lumen	<i>In situ</i>	21.96	1.841	0.981	0.969	<0.001
	<i>Ex situ</i>	16.18	1.330	0.939	0.545	

SD - standard deviation. Shapiro-Wilk test confirmed normal distribution ($W > 0.05$, $p > 0.05$); t-test indicated a significant difference between groups ($p < 0.05$).

Table 6. Microscopic analysis of anatomical structure differences in petiole samples of *Mentha longifolia* collected from the *in situ* and *ex situ* conditions.

Description of anatomical features	<i>In situ</i>	<i>Ex situ</i>
Transverse section of the petiole, ca.tr - capitate trichome, te.tr - tectorial trichome (scale bar: 500 µm)		
Central part of the petiole, pa - parenchyma (scale bar: 200 µm)		
Structure of the vascular tissue, xy - xylem, bas - biological active substances (scale bar: 50 µm)		
Structure of the phloem, ph - phloem (scale bar: 20 µm)		
Lower peripheral region, cl - collenchyma, ep - epidermis, bas - biologically active substances (scale bar: 50 µm)		

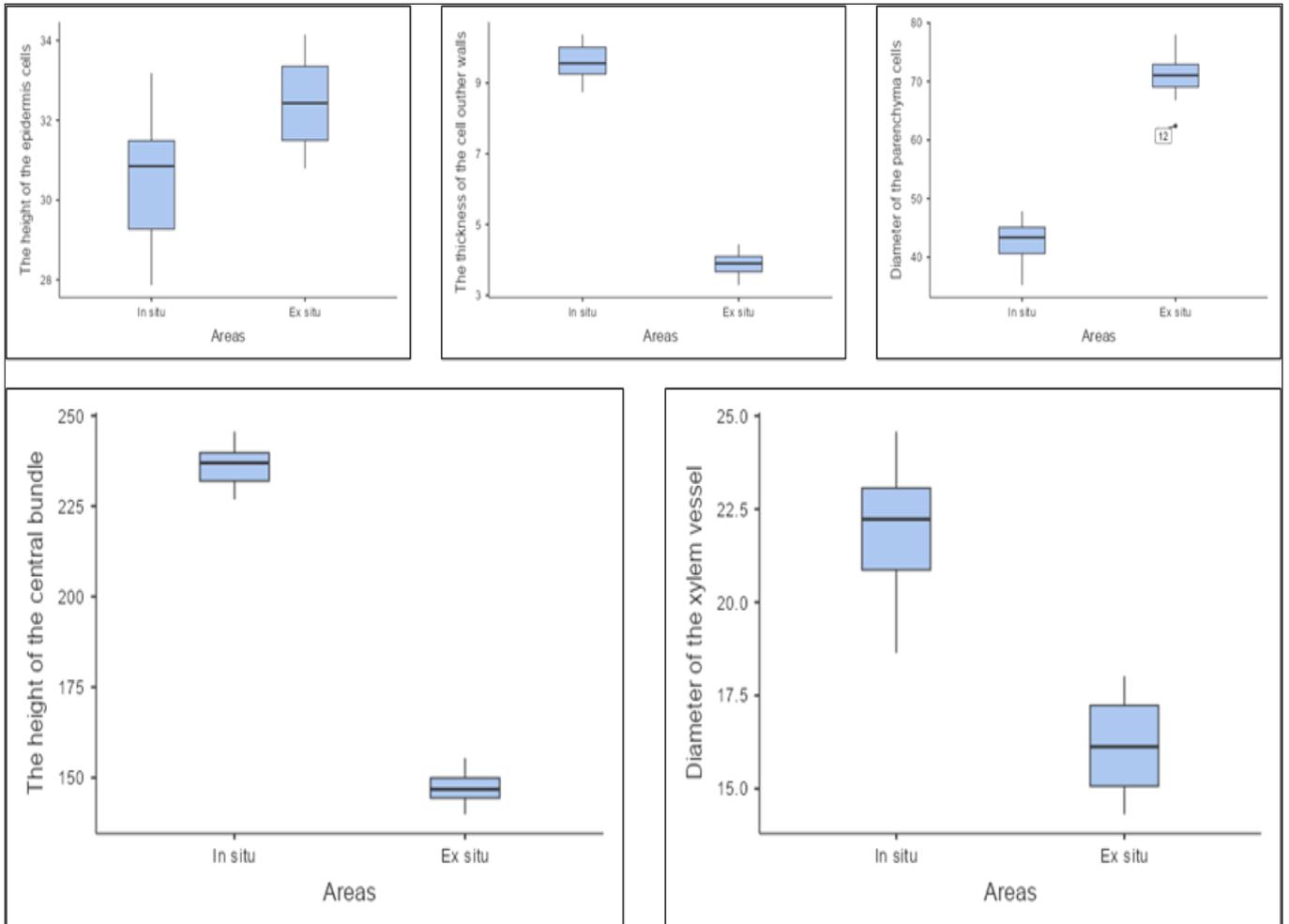


Fig. 6. Comparative box plots of species *Mentha longifolia* petiole measurements from *in situ* and *ex situ* samples.

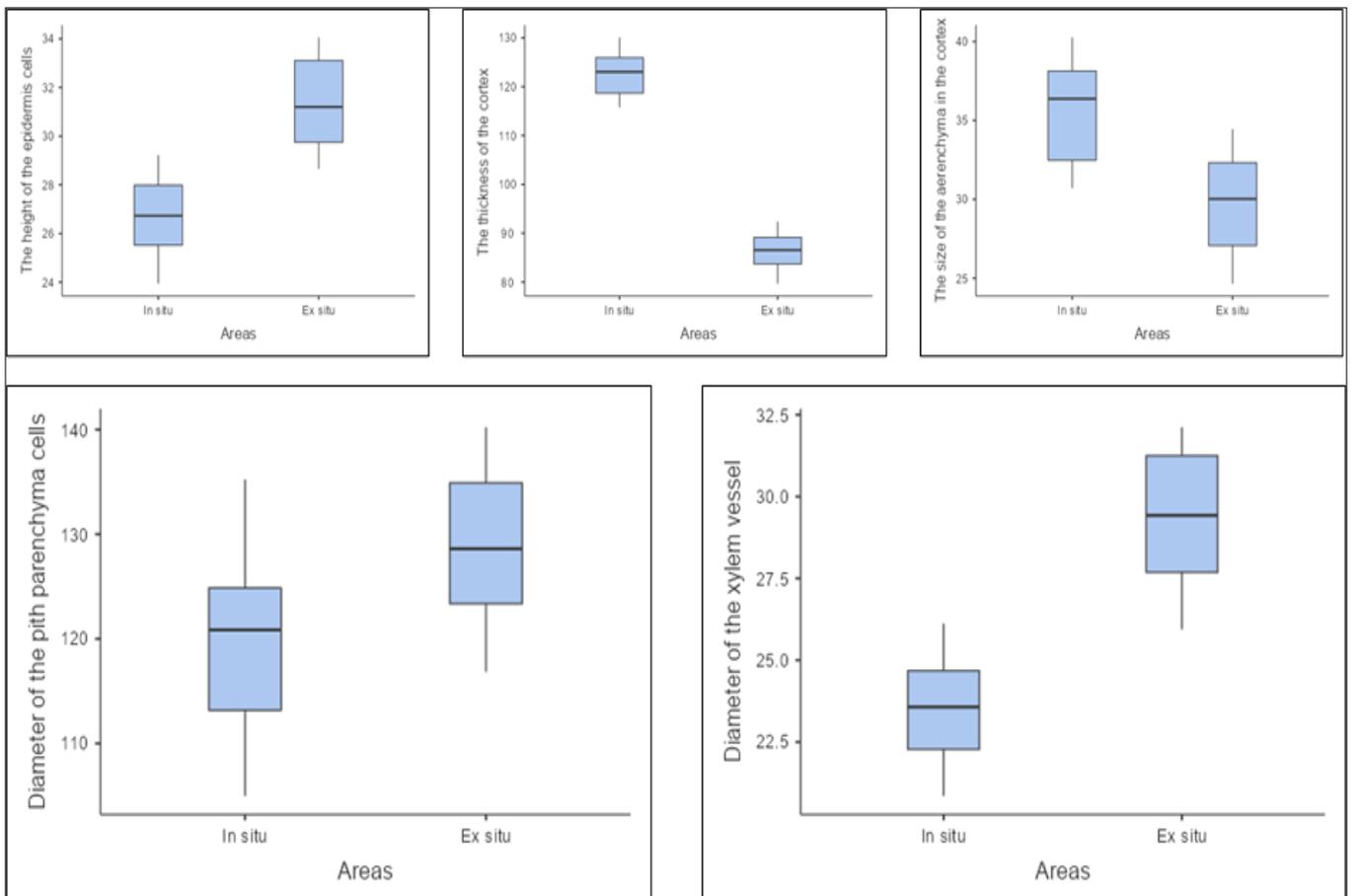


Fig. 7. Comparative box plots of species *Mentha longifolia* stem measurements from *in situ* and *ex situ* samples.

Table 7. Stem tissue measurements and statistical comparison of *in situ* and *ex situ* individuals of the species *Mentha longifolia*

Indicators	Areas	Mean (μm)	SD (μm)	Shapiro-Wilk		Independent Samples T-Test
				W	p	p
The height of the epidermis cells	<i>In situ</i>	26.67	1.781	0.959	0.773	<0.001
	<i>Ex situ</i>	31.38	2.054	0.915	0.317	
The thickness of the cortex	<i>In situ</i>	122.81	5.052	0.944	0.598	<0.001
	<i>Ex situ</i>	86.31	4.106	0.973	0.919	
The size of the aerenchyma in the cortex	<i>In situ</i>	35.57	3.473	0.930	0.444	<0.001
	<i>Ex situ</i>	29.66	3.323	0.960	0.788	
Diameter of the pith parenchyma cells	<i>In situ</i>	120.03	9.268	0.986	0.990	0.039
	<i>Ex situ</i>	128.59	7.987	0.961	0.794	
Diameter of the xylem lumen	<i>In situ</i>	23.54	1.664	0.983	0.978	<0.001
	<i>Ex situ</i>	29.31	2.252	0.928	0.428	

SD - standard deviation. Shapiro-Wilk test confirmed normal distribution ($W > 0.05$, $p > 0.05$); t-test indicated a significant difference between groups ($p < 0.05$).

In *ex situ* specimens, the phloem is bordered externally by a single layer of parenchymal cells, which in turn are overlaid by a thin, continuous layer of small, chloroplast-containing cells forming a belt-like structure across the outer stem surface. At the corners of the stem, protrusions filled with angular collenchyma tissue are clearly visible (27, 28). In *in situ* stems, this collenchyma is directly adjacent to the inner cortical parenchyma. However, in *ex situ* stems, the chloroplast-rich belt-like layer separates the collenchyma from the cortical parenchyma. Considering the number of collenchyma cells and the thickness of the tissue, its micrometric thickness was measured as $157.09 \pm 9.261 \mu\text{m}$ in the *in situ* stem and $142.81 \pm 8.519 \mu\text{m}$ in the *ex situ* stem and this difference was found to be statistically significant ($p < 0.05$). From the corners of the stem extending inward, there are large and well-developed vascular bundles, which appear more compactly arranged in *in situ* plants. Additionally, smaller vascular bundles are distributed along the edge of the pith between these large bundles, with their number being greater in *ex situ* samples. The outer epidermis of the stem is covered by various types of trichomes. In *in situ* specimens, very small capitate trichomes and multicellular tectorial trichomes have been identified through anatomical investigation (29). In contrast, these trichomes are significantly underdeveloped in *ex situ* samples (Table 8). Microscopic observations revealed the presence of a cuticle layer on the epidermis and the formation of epistomatal structures in both the leaf and stem organs of the plant (Fig. 8).

Rhizome

The rhizome of *M. longifolia* possesses a large central pith, around which a well-developed vascular system is observed in the *in situ* samples. The xylem tissue in these samples is notably thicker and contains a greater number of vessel elements and libriform fibres. Accordingly, the quantity and thickness of the phloem tissue are also higher in the *in situ* specimens. An endodermal layer is observed at the cortex-facing edge of the phloem, bordered externally by cortical cells. The cortical cells in *in situ* rhizomes are more uniform in shape and are arranged more compactly. Especially near the outer surface of the rhizome, these tissues form reticulated patterns with aerenchymatous air spaces (Fig. 5C, 5D). In *ex situ* samples, both the number and size of these aerenchyma spaces are reduced (Table 9, Fig. 9). The cortical cells in these samples appear more irregular in shape and loosely arranged. Microscopic observations reveal that the rhizome anatomy exhibits features of both root and stem structures; however, it is of stem origin and structurally more similar to stems (30, 31). Parenchymatous tissue dominates the central

region. Despite its stem origin, the rhizome has acquired certain root-like features due to its subterranean lifestyle (32, 33). Being a perennial species, the plant has undergone secondary growth and developed a periderm.

The parenchyma cells forming the pith are larger in size compared to the cortical cells. Unlike the *in situ* rhizomes, the *ex situ* rhizomes exhibit a better-developed pith parenchyma. In *in situ* samples, the pith cells are more densely packed, with relatively less thickening of the cell walls. One distinct anatomical feature observed in the rhizome of *M. longifolia* is the punctate-porous appearance of the parenchyma cells (Table 10).

Root

In both *ex situ* and *in situ* specimens of *M. longifolia*, the formation of secondary structural elements in the central cylinder of the root has been initiated. The central cylinder is surrounded by the endodermis, composed of a single layer of cells arranged in a ring, which functions as a selective barrier regulating the transport of substances between the cortex and the stele. In the *ex situ* sample, the quantity of xylem is notably higher. Specifically, the secondary xylem derived from the cambium is thicker and contains a greater number of vessel elements. Xylem vessels are generally larger in diameter in the *ex situ* specimens (Table 11, Fig. 10). However, when examining the phloem, it appears somewhat thicker in the *in situ* sample compared to the *ex situ* one. The endodermis merges externally with the mesodermis, which is thicker in the *ex situ* specimen. Due to the loose arrangement of parenchyma cells in this layer, aerenchymatous spaces have developed in some areas (Table 12). The mesodermal cells are more densely packed near the outer exodermal layer. The exodermis is composed of large cells with suberized walls. Suberization is more pronounced in the exodermal and epidermal cells of the *in situ* specimens. In contrast, the suberized layer is relatively less developed in the *ex situ* specimens.

Discussion

Anatomical analysis revealed that *M. longifolia* specimens grown under *in situ* conditions exhibit enhanced accumulation of ergastic and constitutional substances within internal structures. Additionally, idioblastic green pigmentation is more pronounced in parenchyma cells, indicating a richer metabolic profile. This idioblast formation is likely associated with a high concentration of chloroplasts or the accumulation of specific metabolites in vacuoles, such as flavonoids or terpenoids, in both photosynthetic and

Table 8. Microscopic analysis of anatomical structure differences in stem samples of *Mentha longifolia* collected from the *in situ* and *ex situ* conditions.

Description of anatomical features	<i>In situ</i>	<i>Ex situ</i>
Transverse section of the stem, te.tr - tectorial trichome, pi - pith (scale bar: 500 μ m)		
Ridge region of the stem, xy - xylem, a.cl - angular collenchyma, ca.tr - capitate trichome (scale bar: 400 μ m)		
Inter-bundle region, ib - idioblast, p.e - parenchymatic excretion, ph - phloem (scale bar: 200 μ m)		
Angular collenchyma (scale bar: 50 μ m)		
Cortex, ep - epidermis, l.cl - lacunar colenchyma, ae - aerenchyma, ch - chlorenchyma, ph - phloem (scale bar: 50 μ m)		
Tectorial trichomes (scale bar: 50 μ m)		

"7 μ m" shown on the first image indicates the section thickness.

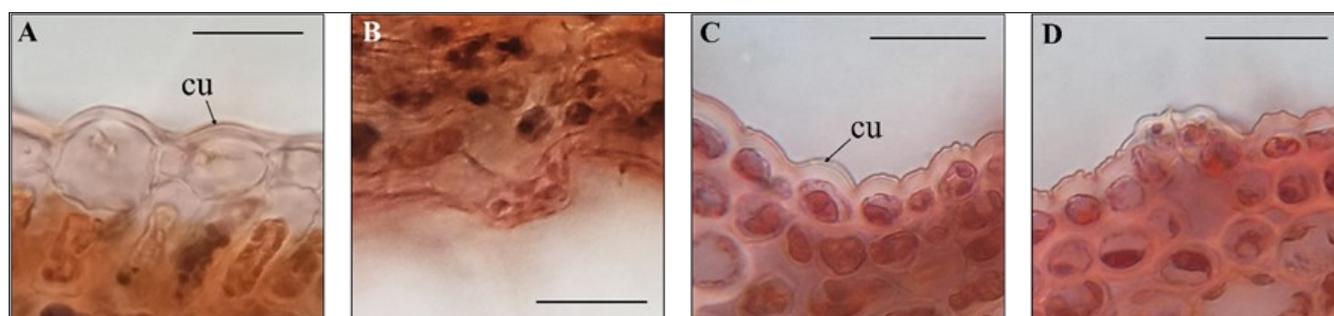


Fig. 8. Cuticle layer and stomata on the epidermis. A-B. Leaf; C-D. Stem; cu-cuticle; scale bars: 20 μ m.

Table 9. Rhizome tissue measurements and statistical comparison of *in situ* and *ex situ* individuals of the species *Mentha longifolia*

Indicators	Areas	Mean (µm)	SD (µm)	Shapiro-Wilk		Independent Samples T-Test
				W	p	p
The size of the aerenchyma in the cortex	<i>In situ</i>	51.51	4.955	0.970	0.895	<0.001
	<i>Ex situ</i>	43.29	4.014	0.975	0.933	
Diameter of the cortex parenchyma cells	<i>In situ</i>	21.87	3.012	0.970	0.894	<0.001
	<i>Ex situ</i>	39.43	3.691	0.927	0.423	
Diameter of the pith parenchyma cells	<i>In situ</i>	58.73	3.956	0.957	0.746	<0.001
	<i>Ex situ</i>	78.08	4.893	0.973	0.916	

SD - standard deviation. Shapiro-Wilk test confirmed normal distribution ($W > 0.05$, $p > 0.05$); t-test indicated a significant difference between groups ($p < 0.05$).

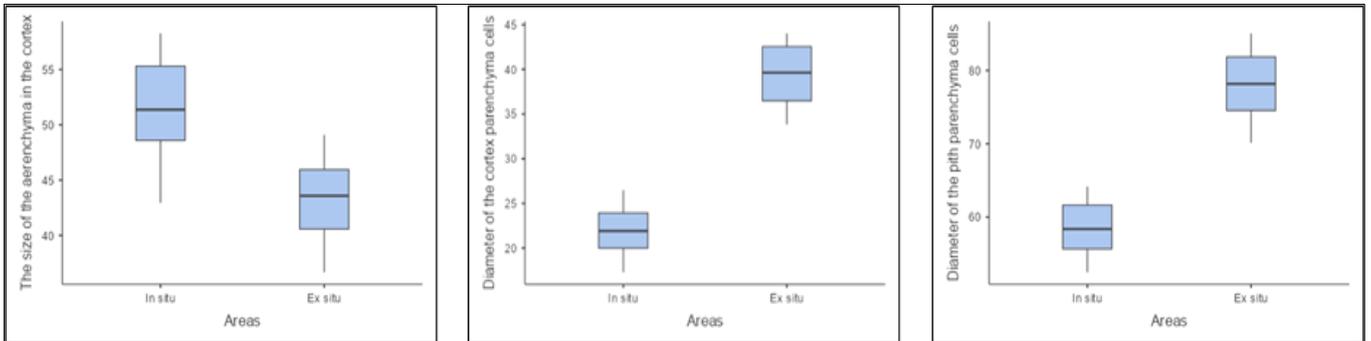


Fig. 9. Comparative box plots of species *Mentha longifolia* rhizome measurements from *in situ* and *ex situ* samples.

Table 10. Microscopic analysis of anatomical structure differences in rhizome samples of *Mentha longifolia* collected from the *in situ* and *ex situ* conditions

Description of anatomical features	<i>In situ</i>	<i>Ex situ</i>
Transverse section of the rhizome (scale bar: 500 µm)		
A part of the rhizome, ph - phloem, xy - xylem, co - cortex (scale bar: 200 µm)		
Cortex tissue forming aerenchyma, ae - aerenchyma, pr - periderm (scale bar: 50 µm)		
Pith parenchyma, pi-pith (scale bar: 200 µm)		
Porous pit-like arrangement on the walls of the parenchyma cells (scale bar: 50 µm)		

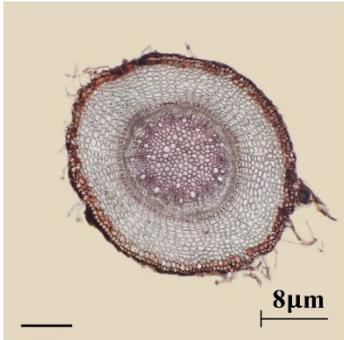
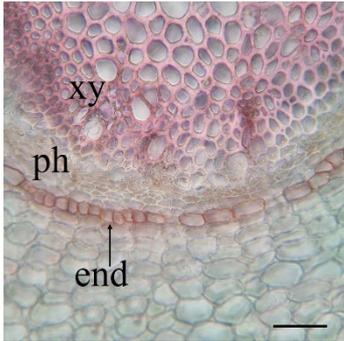
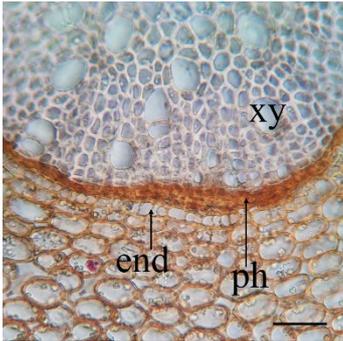
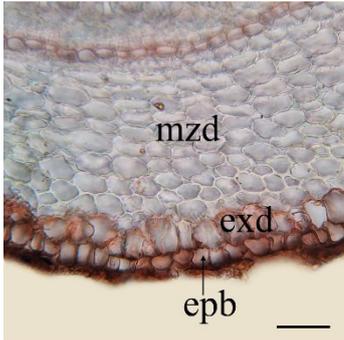
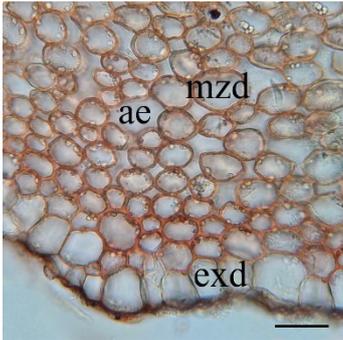
“8 µm” shown on the first image indicates the section thickness.

Table 11. Root tissue measurements and statistical comparison of *in situ* and *ex situ* individuals of the species *Mentha longifolia*

Indicators	Areas	Mean (μm)	SD (μm)	Shapiro-Wilk		Independent Samples T-Test
				W	p	p
The height of the epiblem cells	<i>In situ</i>	17.97	1.962	0.916	0.321	
	<i>Ex situ</i>	NaN	NaN	NaN	NaN	
The height of the exodermis cells	<i>In situ</i>	33.12	3.013	0.947	0.632	<0.001
	<i>Ex situ</i>	45.50	3.670	0.937	0.518	
Diameter of the mesodermis cells	<i>In situ</i>	25.50	1.967	0.915	0.316	<0.001
	<i>Ex situ</i>	32.73	2.498	0.963	0.814	
The height of the endodermis cells	<i>In situ</i>	8.49	0.573	0.912	0.298	<0.001
	<i>Ex situ</i>	10.39	0.541	0.945	0.610	
Diameter of the xylem lumen	<i>In situ</i>	24.19	2.247	0.955	0.730	<0.001
	<i>Ex situ</i>	29.05	2.955	0.946	0.616	

SD - Standard deviation. NaN - Not a Number (Tissue absent in the sample). Shapiro-Wilk test confirmed normal distribution ($W > 0.05$, $p > 0.05$); t-test indicated a significant difference between groups ($p < 0.05$).

Table 12. Microscopic analysis of anatomical structure differences in root samples of *Mentha longifolia* collected from the *in situ* and *ex situ* conditions

Description of anatomical features	<i>In situ</i>	<i>Ex situ</i>
Transverse section of the root (scale bar: 200 μm)		
A part of the central cylinder, end - endodermis, xy - xylem, ph - phloem (scale bar: 50 μm)		
Cortex, mzd - mezodermis, ae - aerenchyma, exd - exodermis, epb - epiblem (scale bar: 50 μm)		

"8 μm " shown on the first image indicates the section thickness.

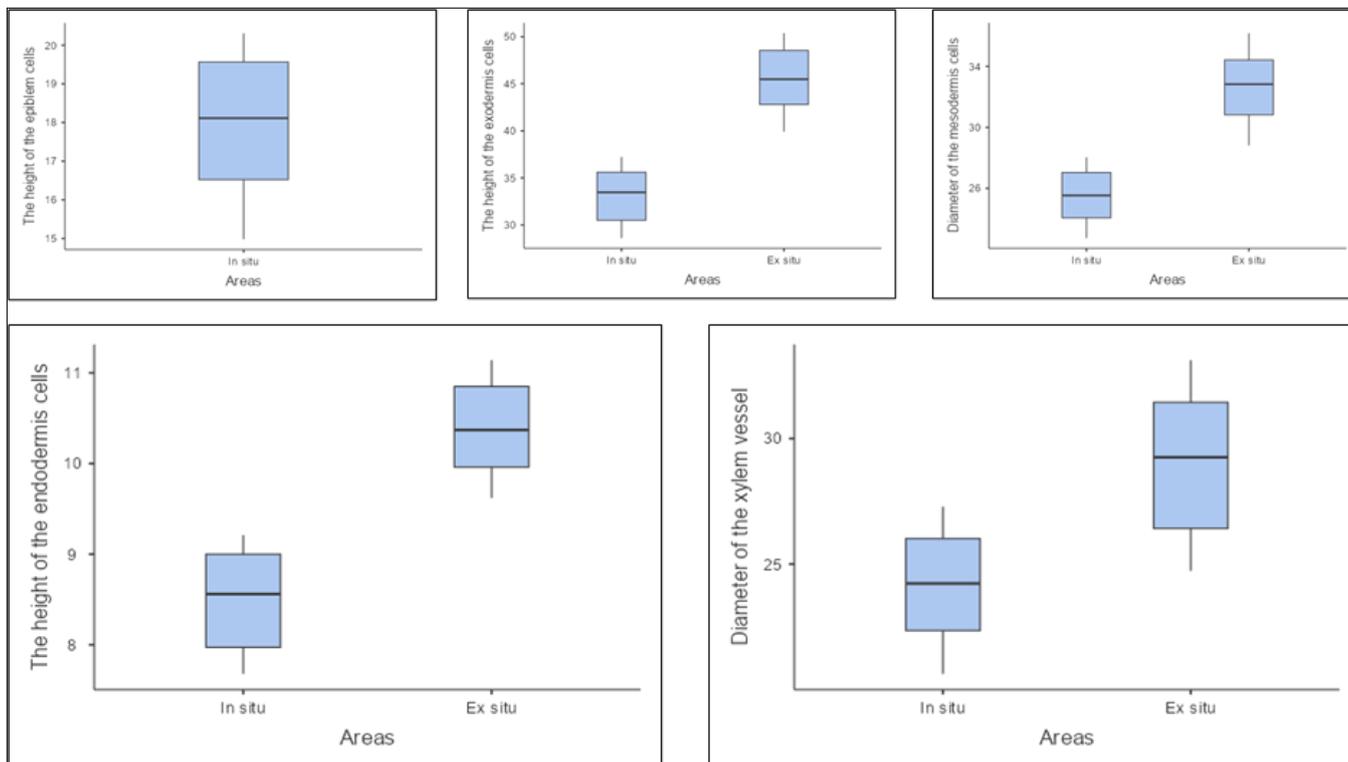


Fig. 10. Comparative box plots of species *Mentha longifolia* root measurements from *in situ* and *ex situ* samples.

carnivorous plants and also in tree species (34, 35). In this regard, chromatographic analysis by pharmaceutical experts is recommended to elucidate the nature of these structures. In the leaves and stems of the *in situ* specimens, conical, tectorial and capitate trichomes were observed, while only conical and tectorial trichomes were detected in the leaves and stems of *ex situ* samples. Microscopic analysis confirmed the accumulation of specific compounds within the capitate trichomes, which is considered an indicator of their secretory activity in *in situ* specimens (Tables 3, 4).

The conical trichomes present in the plant help prevent water loss, regulate transpiration and play a role in adaptation under high temperature and drought conditions. They also contribute to the secretion of essential oils (36, 37). In *M. longifolia*, the denser and slender, elongated trichomes observed in the *in situ* specimens indicate a defensive mechanism to reduce water loss. In contrast, the reduced trichome density in the leaves of *ex situ* specimens represents a structural adaptation formed under optimal conditions, where water loss and mechanical stress are minimal. The presence of a thin cuticular layer on the epidermis of the stem during histo-anatomical and biochemical analysis of *M. longifolia* in the phenophase stage (27). However, in our study, this layer was observed to be thicker on the epidermis of both the leaves and stems of *in situ* specimens (Fig. 8A–C). Previous authors classified foliar trichomes into two main types. Tectorial trichomes are multicellular structures formed by a linear arrangement of elongated cells ending in a sharp tip. Secretory trichomes are fewer in number and shorter, characterised by a unicellular head supported by a multicellular stalk. Our findings support these observations, particularly the dense distribution of tectorial trichomes on *in situ* leaves, in contrast to their sparser presence in *ex situ* samples. Secretory trichomes displayed diverse morphologies and biologically active compounds were found within their cells as well as in some tectorial trichomes, indicating intensive secretory function in *in situ* plant parts.

Research indicates that the presence of protruding epistomatic stomata. However, in our study, such stomata were observed on the leaves and stems of both *in situ* and *ex situ* samples under microscopic examination (Fig. 8B–D). In their study of five different populations of *M. Longifolia*, they determined that the yield and composition of essential oils varied across vegetative stages but remained relatively stable during flowering (12). While their research identified the composition of biologically active components such as hydrocarbon monoterpenes (limonene, sabinene, myrcene, etc.), it did not provide detailed microscopic localisation or distribution of these metabolites within specific tissue groups. This limits understanding of their functional roles and the identification of optimal plant parts for raw material use.

Conversely, our study visualised the accumulation of these active compounds across various tissue types - parenchyma, collenchyma, sclerenchyma, vascular elements and secretory structures - thus enabling insights into their biosynthesis and accumulation dynamics. This integrative approach, combining phytochemical and anatomical-histochemical analysis, enhances the scientific relevance of the research. Coordinated mapping of metabolite accumulation through microscopy offers new data on their tissue-specific value and functional significance.

Research indicates four *Mentha* species, including two subspecies of *M. longifolia* and observed both glandular and non-glandular trichomes on leaf surfaces (25). In our microscopic observations, *ex situ* specimens exhibited non-glandular tectorial and conical trichomes, whereas *in situ* specimens also showed the formation of small-capitate trichomes. Additionally, foreign researchers reported the presence of collenchyma tissue in the subepidermal zones of the midrib region of the leaf, which was also observed in our specimens. Among the studied species, *M. longifolia* subspecies exhibited a notably compact arrangement of palisade and spongy parenchyma, a finding confirmed by our own microscopic analyses. Both *in situ* and *ex situ* samples demonstrated a compact structure in these tissue layers.

Through comparative anatomical analysis, the stem structure and vascular system of the studied specimens were found to be consistent with previous descriptions in the literature. However, both *in situ* and *ex situ* specimens in our study exhibited more developed vascular and mechanical tissues, whereas previously studied samples showed more intensive development of ground tissue. This difference is likely related to Azerbaijan's mountain and temperate continental climate, characterised by significant seasonal temperature fluctuations. Rich mineral soil and seasonally variable water regimes promote a blend of hygrophytic and mesophytic traits, leading to enhanced vascular development. From an ecophysiological perspective, adaptation to environmental stressors such as wind pressure and humidity fluctuations results in the increased development of mechanical tissues in the stem and petiole, thereby enhancing plant resilience (38, 39).

The study on the anatomical structure of the shoots of *Mentha × villosa* Huds. indicates that the stem possesses a wide pith composed of cells of various sizes, with four vascular bundles located at the corners (40). This feature represents a general structural characteristic of the genus and was also recorded in both ecotypes of the species examined in the present study. The authors further noted the presence of substomatal air cavities beneath the stomata on the leaf epidermis; similarly, in the *in situ* and *ex situ* leaf and stem samples of *M. longifolia* analysed in our research, small substomatal air cavities were observed within the stomatal regions. In addition, previous studies stated that in *Mentha × villosa*, the leaf mesophyll is differentiated into one or two layers of palisade parenchyma and three to five layers of spongy parenchyma (40). In our study, *M. longifolia* showed comparable features: in *in situ* leaf samples, the palisade parenchyma consisted of a clearly defined single layer of elongated cells, while the spongy parenchyma was mainly composed of three compact layers. In the *ex situ* specimens, the palisade parenchyma was also primarily single-layered, though in some areas a weakly developed second layer of cells was observed. The spongy parenchyma in these samples consisted of three to four layers, as confirmed by microscopic analyses (Fig. 5A & B). Based on the obtained results, the structural variations in the mesophyll between *in situ* and *ex situ* specimens of *M. longifolia* can be interpreted as manifestations of the species' adaptive capacity to different ecological conditions - namely, its anatomical plasticity. In the *in situ* specimens, the compact arrangement of spongy parenchyma and the presence of a single palisade cell layer indicate adaptation to conditions of higher light intensity typical of natural habitats. Such a structure facilitates more efficient use of light energy and helps reduce transpiration. Conversely, the mesophyll characteristics observed in the *ex situ* specimens may reflect adaptation to lower light levels in shaded environments, as this type of tissue organisation promotes greater internal light diffusion and facilitates gas exchange.

The "punctate-porous" structure observed in the parenchyma cells of the rhizome can be interpreted as a formation associated with a high concentration of metabolites that constitute the phytotherapeutic basis of the plant. In general, *M. longifolia* is known to belong to the group of essential oil-bearing plants. Accordingly, the observed structure can be related to the accumulation of essential oils or the development of secretory cells (41). In these oil-accumulating cells, the expansion of vacuoles compresses the protoplast, leading to the formation of visible holes or porous structures in the cell wall.

Anatomical analyses also revealed that the cortical aerenchyma in the rhizome of *M. longifolia* was smaller and less abundant in *ex situ* samples (Fig. 5C & D). These differences were statistically supported by morphometric data. Aerenchyma serves as an adaptive mechanism that facilitates oxygen diffusion in hypoxic and waterlogged soils, thereby supporting stable metabolic functions. The development of aerenchyma in the *in situ* mountain populations may be driven by poor soil drainage and specific microclimatic conditions. In such environments, aerenchyma enhances oxygen transport to tissues and contributes to water regulation. In contrast, the reduced aerenchyma in *ex situ* samples may reflect the more stable environmental conditions and reduced selective pressure for aeration tissue development. This demonstrates that ecological variation can induce anatomical differences even among genetically identical plants, exemplifying ecotypic variation and phenotypic plasticity. In the *ex situ* specimens of *M. longifolia*, the enlargement of parenchyma cells in all examined organs likely reflects structural adaptation to variable ecological conditions, representing the eco-physiological plasticity of cell size. This may be associated with higher turgor pressure and more stable water and mineral availability (42-44).

In *ex situ* conditions, the epiblem layer in *M. longifolia* roots was degraded, possibly due to differences in soil structure, water balance and aeration. The exodermis, acting as a temporary protective layer, was more prominent. *In situ* roots retained the epiblem layer, suggesting that in the relatively aerated and moist soil of the *ex situ* environment, the exodermis assumes a temporary protective role. The more favourable conditions of the *ex situ* environment may stimulate accelerated vegetative growth, with increased activity in the root apical meristem and pericycle cells promoting early secondary development. Thus, faster root growth under *ex situ* conditions initiates earlier formation of the phellogen and vascular cambium, leading to the transition to secondary structure. In contrast, the persistent humidity and mist in the mountainous *in situ* habitat may prolong the presence of the epiblem. Its eventual loss and replacement by periderm in *ex situ* specimens reflects the early stages of secondary growth. The intense suberization of exodermis and epiblema cells observed in the roots of the *in situ* specimens represents an adaptation formed in response to environmental conditions (45). These findings collectively underscore the anatomical adaptations of *M. longifolia* to diverse ecological conditions and highlight the influence of microclimate on internal plant structures.

Conclusion

The findings of the present study demonstrate that *M. longifolia* exhibits distinct ecological-anatomical adaptation strategies in response to varying environmental conditions under *in situ* and *ex situ* growth settings. As an indicator of ecosystem variability, it was determined that the pharmaco-anatomical stability of the plant is partially maintained under *ex situ* conditions; however, certain adaptive differences were also observed. Differences in parenchyma cell size between ecotypes (a - *in situ*, b - *ex situ*) were recorded as follows: leaf - a: $31.52 \pm 2.279 \mu\text{m}$, b: $37.51 \pm 2.465 \mu\text{m}$; petiole - a: $42.76 \pm 3.701 \mu\text{m}$, b: $70.86 \pm 4.402 \mu\text{m}$; stem pith parenchyma - a: $120.03 \pm 9.268 \mu\text{m}$, b: $128.59 \pm 7.987 \mu\text{m}$; rhizome cortex parenchyma - a: $21.87 \pm 3.012 \mu\text{m}$, b: $39.43 \pm 3.691 \mu\text{m}$; rhizome pith parenchyma - a: $58.73 \pm 3.956 \mu\text{m}$, b: $78.08 \pm 4.893 \mu\text{m}$; root mesodermis tissue - a: $25.50 \pm 1.967 \mu\text{m}$, b: $32.73 \pm 2.498 \mu\text{m}$. Variations were also recorded

in vascular elements: xylem lumen diameter – leaf - a: 11.74 ± 0.889 μm , b: 22.68 ± 1.521 μm ; petiole - a: 21.96 ± 1.841 μm , b: 16.18 ± 1.330 μm ; stem - a: 23.54 ± 1.664 μm , b: 29.31 ± 2.252 μm ; root - a: 24.19 ± 2.247 μm , b: 29.05 ± 2.955 μm ; vascular bundle size: leaf - a: 123.77 ± 5.483 μm , b: 130.64 ± 5.245 μm ; petiole - a: 236.23 ± 5.852 μm , b: 147.29 ± 4.902 μm . These micrometric results fully support the observations and statistically significant structural differences between these ecotypes were confirmed using statistical tests ($p < 0.05$). In the leaves of *in situ* *M. longifolia* specimens, the density of long tectorial, small conical and capitate trichomes was higher compared to *ex situ* specimens, which is considered an adaptive mechanism in the extreme conditions of the mountainous ecosystems of the Lesser Caucasus. The functional activity of parenchymatic excretion, the “punctate-porous” cell structure and aerenchyma tissue (stem cortex - a: 35.57 ± 3.473 μm , b: 29.66 ± 3.323 μm ; rhizome cortex - a: 51.51 ± 4.955 μm , b: 43.29 ± 4.014 μm) was observed in *in situ* specimens. In the roots of *M. longifolia*, the exodermis functions as a temporary protective tissue under *ex situ* conditions, whereas *in situ* specimens retain a functional epiblem as the primary dermal tissue. These findings offer a fundamental comparative anatomical model confirming the role of ecological anatomy in plant adaptation to environmental factors, thus possessing both scientific and practical significance. The results of this study serve as markers in assessing plant adaptation potential to climate variability, particularly in the context of biodiversity conservation, plant resilience mechanisms across diverse ecosystems and ecological sustainability. The outcomes also represent a unique contribution to contemporary global initiatives such as the Convention on Biological Diversity (COP), by providing empirical evidence for understanding plant resilience under changing environmental conditions. Therefore, this research holds substantial theoretical and practical value in the development of future climate adaptation strategies.

Authors' contributions

AS conceived and designed the study, performed the experiments, analyzed and interpreted the data and prepared the manuscript. All authors read and approved the manuscript.

Compliance with ethical standards

Conflict of interest: Author does not have any conflict of interests to declare.

Ethical issues: None

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