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Adaptive morpho-anatomical traits of *Euphorbia yaroslavii* populations in the Zailiysky Alatau, Kazakhstan

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Abstract. *Turgara Z, Ametov A, Kenesbay A, Imanova E, Sypabekkyzy G, Osmonali B. 2026. Adaptive morpho-anatomical traits of* Euphorbia yaroslavii *populations in the Zailiysky Alatau, Kazakhstan. Biodiversitas 27 (6): d270604. https://doi.org/10.13057/biodiv/d270604.* *Euphorbia yaroslavii* is a narrow-range endemic of the northern Tien Shan, restricted to foothill steppe and clayey habitats of the Zailiysky Alatau, Kazakhstan and is insufficiently studied in terms of morphological and anatomical variability. This study aimed to evaluate interpopulation variation in morphological, anatomical, and seed micromorphological traits of *E. yaroslavii* under contrasting ecological conditions. Three spatially isolated populations were analyzed using a comparative approach that included morphometric measurements of vegetative and generative organs, anatomical investigation of leaf, stem, and root structures, and scanning electron microscopy of seed surfaces. The results showed pronounced interpopulation differentiation mainly in vegetative morphology and anatomical structure. The greatest variability was recorded in leaf thickness, mesophyll organization, and development of conductive tissues, reflecting habitat-related environmental differences. In contrast, generative traits, including cyathium and seed dimensions, were relatively stable. ANOVA confirmed significant differences ($p<0.05$) in most vegetative and anatomical parameters, whereas reproductive traits showed no significant differences. Correlation analysis revealed coordinated variation among structural traits of different organs. Population differentiation in *E. yaroslavii* is primarily expressed in vegetative and anatomical features, while reproductive traits remain stable. These findings provide a quantitative framework for understanding adaptive variation and support population-based conservation strategies for this endemic species.

Keywords: Endemic plants, *Euphorbia yaroslavii*, leaf structure, phenotypic plasticity, Scanning Electron Microscopy

INTRODUCTION

The genus *Euphorbia* L. (Euphorbiaceae) comprises more than 2,000 species distributed across deserts, steppes, Mediterranean regions, and mountain systems worldwide (Riina et al. 2013; Pahlevani et al. 2017; Turgara et al. 2025; POWO 2026). Molecular phylogenetic studies recognize four major subgenera, namely *Esula*, *Euphorbia*, *Chamaesyce*, and *Athymalus*, which reflect evolutionary diversification across contrasting climatic zones (Riina et al. 2013; Pahlevani et al. 2017). Subgenus *Esula* is widely represented in Eurasia, includes perennial herbaceous species adapted to seasonally dry habitats and characterized by xeromorphic vegetative traits and specialized cyathia (Bolaji et al. 2014).

In Kazakhstan, approximately 49 *Euphorbia* species occur in deserts, steppes, foothills, and mountain regions (Baitenov 2001; Turgara et al. 2025; POWO 2026). *Euphorbia yaroslavii* Poljakov belongs to the subgenus *Esula*. It is a narrow endemic restricted to the northern Tien Shan and is confined to clayey foothill slopes of the Zailiysky Alatau, mainly within the Kaskelen and Chemolgan gorges (Turgara et al. 2025). The species inhabits steppe-like communities on compacted loamy and clay substrates, where short-term spring moisture is followed by prolonged summer drought. Based on the morphological characteristic, *E. yaroslavii* is distinguished by a tuberously thickened subterranean stem, dense foliage, and terminal and axillary inflorescences. The thickened underground stem functions as a storage organ that supports early vegetative growth under fluctuating moisture conditions (Kokoreva et al. 2017). Similar drought-adaptive structural features have been described in other xerophytic *Euphorbia* species, where underground organs and leaf xeromorphy contribute to seasonal stress tolerance (Horn et al. 2014; Ramos et al. 2020).

Unlike some economically valuable species of the genus, *E. yaroslavii* has no documented medicinal or ornamental use and is primarily significant as a local endemic taxon. Its restricted range and proximity to the urban area of Almaty expose populations to grazing, recreational disturbance, and infrastructure development. Kokoreva et al. (2017) reported population size and age structure of *E. yaroslavii* and revealing the predominance of generative individuals while also indicating increasing habitat fragmentation. However, detailed analyses of its morphological and anatomical variability remain absent.

Morphological and anatomical traits in *Euphorbia* have been shown to reflect ecological differentiation. Studies from Mediterranean, North African, and Central Asian regions demonstrate that vegetative characters, such as leaf thickness, mesophyll organization, and development of conductive tissues often exhibit pronounced variability along environmental gradients, including soil texture and moisture availability (Bolaji et al. 2014; Moustafa et al. 2016). In contrast, generative traits, such as cyathium dimensions and seed size, tend to be more conservative. Seed micromorphology examined using scanning electron microscopy has also proven informative for structural differentiation within the genus (Ghosh et al. 2019). Nevertheless, most available data concern widespread taxa, whereas integrative studies of narrow endemic species remain limited.

Understanding the balance between vegetative plasticity and reproductive stability is essential for evaluating adaptive capacity under environmental change, mainly for endemic species confined to environmentally heterogeneous foothill ecosystems. Morphometric, micromorphological traits, and anatomical in *E. yaroslavii* have not previously been compared across spatially isolated populations. This gap limits assessment of population-level differentiation and identification of structural traits associated with local habitat conditions. Therefore, this study aimed to evaluate morphological, anatomical, and seed micromorphological variability of *E. yaroslavii* across spatially isolated populations occurring under contrasting environmental conditions of the Zailiysky Alatau. We tested whether vegetative traits exhibit greater interpopulation variability than generative traits, whether anatomical features related to photosynthetic and conductive tissues show the strongest differentiation, and whether structural traits of different organs vary in a coordinated manner. This integrative analysis provides a quantitative basis for assessing population differentiation in a narrow endemic species and contributes to understanding morpho-anatomical variability in xerophytic *Euphorbia* of Central Asia.

MATERIALS AND METHODS

Study area

The study was conducted in three mountain gorges of the Zailiyskiy Alatau ridge, Almaty Region, southeastern Kazakhstan, an area characterized by pronounced altitudinal zonation, strong ecological gradients, and high habitat heterogeneity (Figure 1; Table 1). Distribution of *E. yaroslavii* is restricted to several localities within the Kaskelen, Chemolgan, and adjacent gorges, where it occurs on clayey and loamy slopes within steppe-like communities. The species has not been recorded outside this limited geographic range, which emphasizes its regional endemism and ecological specificity (Kubentayev et al. 2024; Aldassugurova et al. 2025; Karabalayeva et al. 2025).

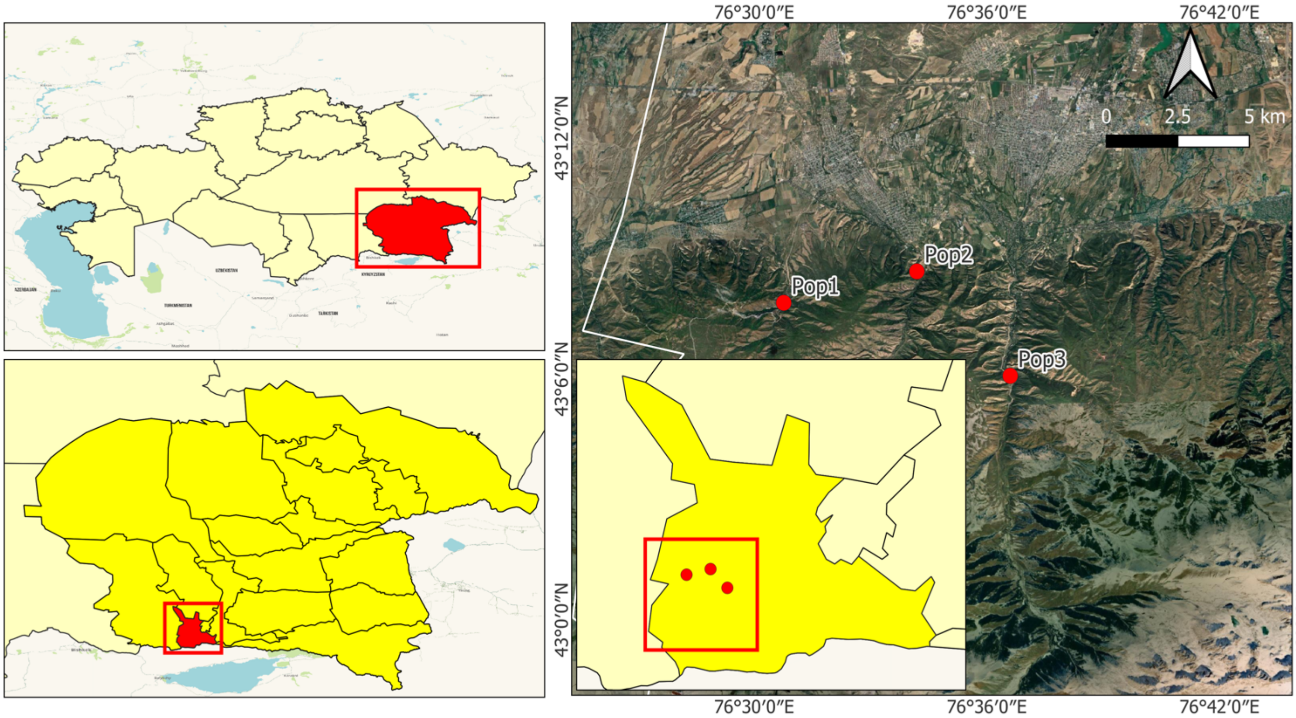

Figure 1. Study sites of Almaty Region, southeastern Kazakhstan. The spatial distribution of all populations and sampling points was mapped using QGIS software (2024)

Table 1. Geographical coordinates and elevation gradient of *Euphorbia yaroslavii* populations

Population (Pop)	Location	Elevation (m asl)	Coordinates (N, E)	Note
Pop1	Shamalgan rural district, Karasai district, Zailiyskiy Alatau, Almaty Region, southeastern Kazakhstan	1276	43° 07′ 53.72″ N, 76° 30′ 45.79″ E	Moderately mesic site in the Ushkonyr Gorge with weak anthropogenic disturbance. Upper foothill zone with moderately steep south-southwestern slopes. Clay-loam soils and steppe-shrub vegetation with xerophytic grasses and forbs. Relatively stable microhabitat with higher moisture retention compared to Pop2.
Pop2	Shamalgan rural district, Karasai district, Zailiyskiy Alatau, Almaty Region, southeastern Kazakhstan	1171	43° 08′ 40.61″ N, 76° 34′ 11.83″ E	Dry and disturbed site in the Shamalgan Gorge, characterized by heterogeneous microrelief and strong anthropogenic pressure. Lower foothill zone with gently inclined slopes and high insolation. Heavy clay soils with reduced drainage and sparse steppe vegetation. Represents the most stress-prone population.
Pop3	Zhandosovsky rural district, Karasay district, Zailiyskiy Alatau, Almaty Region, southeastern Kazakhstan	1315	43° 06′ 04.57″ N, 76° 36′ 36.37″ E	Ecotonal site in the Kaskelen Gorge with heterogeneous environmental conditions. Upper foothill-lower montane transition zone with mixed slope exposure. Loamy to clay-loam soils with seasonal moisture accumulation. More diverse and denser vegetation; relatively low disturbance. Suitable for assessing interpopulation variability.

The three populations were selected as spatially isolated occurrences within the species' distribution. They differ in key environmental parameters, including altitude, slope exposure, soil texture, and anthropogenic impact. These sites capture the main ecological variation within the foothill zone where the species persists. This provides a representative framework for evaluating interpopulation morphological and anatomical differentiation. The geographically separated populations also enable assessment of structural variability under contrasting moisture and substrate conditions. At the same time, all sites remain within the natural ecological amplitude of the species. Such a design is especially important for narrow endemic taxa, as it allows reliable interpretation of adaptive variation and supports conservation planning. Three spatially isolated natural populations were selected along gradients of moisture availability, substrate composition, and anthropogenic impact. During the field expedition, specimens of *E. yaroslavii* were collected from three spatially isolated populations representing different foothill zones of the Zailiysky Alatau (Figure 1).

Procedures

Morphological observation

Plant materials were collected from three natural populations using standard herbarium and population sampling techniques (Sumbembayev et al. 2023). Ten sampling plots of 1 m × 1 m were established in each population to assess morphological variability (Begenov et al. 2015; Bazarov et al. 2023; Tleuberlina et al. 2026), resulting in a total of 30 plots. Within each population, 15 generative individuals were randomly selected for morphometric analysis, resulting in a total sample size of 45 individuals. The same individuals were used for measurements of all vegetative and generative morphological traits to ensure balanced sampling and comparability among populations.

For each of the 16 morphological and 18 anatomical traits, statistical analyses were conducted independently, treating population identity as a fixed-effect factor. For the assessment of interpopulation morphological variability, a set of quantitative vegetative and generative traits was measured. In total, 10 vegetative parameters were analyzed, including the length and width of axillary vegetative shoots, stem leaves, proximal stem leaves, and ray leaves, as well as stem length and diameter. The generative dataset comprised 6 traits, including cyathium length and width, nectary gland length and width, and seed length and width. These characters were selected as informative indicators of structural differentiation and phenotypic variability at the population level (Sumbembayev et al. 2023).

All measurements were taken from mature individuals at the generative stage to ensure comparability among populations. Photographic documentation and morphometric measurements were performed using a Levenhuk DTX RC4 digital microscope with calibrated measurement software, which allowed precise analysis of small reproductive structures and minimized measurement error (Kubentayev et al. 2022; Sumbembayev et al. 2023, 2025a,b; Abdildanov et al. 2025; Islamgulova et al. 2025; Kenesbay et al. 2025). The selected trait complex provides a consistent basis for evaluating interpopulation variability and for comparing the degree of differentiation between vegetative and reproductive structures in *E. yaroslavii*.

Seed micromorphology was examined using a SEM2000 scanning electron microscope (China). General seed morphology was documented at low magnification, followed by detailed examination of testa relief and surface structures at higher magnifications, allowing visualization of surface elements in the micrometer range.

Anatomical observation

Five generative individuals per population were selected for anatomical analysis, resulting in a total of 15 individuals across the three studied populations. From each individual, samples of the leaf blade, stem, and root were collected. Plant material was fixed in 60-70% ethanol immediately after collection to preserve tissue structure and prevent cellular degradation. Transverse sections of vegetative organs were prepared from histological paraffin-embedded samples. Sectioning was performed using a rotary semi-automatic microtome (MEDITE M530) at a thickness of 40 μm, which ensured structural integrity of tissues and suitability for detailed anatomical analysis. The preparation of permanent slides followed standard botanical microtechnique protocols commonly applied in plant anatomical studies (Ruzin 1999).

Eight transverse sections per individual were analyzed for each organ. Thus, anatomical analysis was based on 40 sections per organ per population (5 individuals × 8 sections), corresponding to 120 transverse sections per population and 360 sections in total for all three populations. Sections were stained with a safranin-fast green combination to differentiate lignified and non-lignified tissues; in some cases, observations were additionally performed on unstained sections for structural comparison (Osmonali et al. 2025). Prepared anatomical sections were examined under a Levenhuk Zoom & Joy microscope (China), and microphotographs were obtained using a Levenhuk D740T 5.1 MP digital camera with LevenhukLite software (Osmonali et al. 2025). For each transverse section, quantitative measurements were obtained for epidermis thickness, mesophyll layer dimensions, vascular bundle size, and supporting tissues. Mean values and standard errors were calculated for each anatomical parameter based on measurements from all analyzed sections. Anatomical descriptions and interpretation were conducted using recent literature on closely related taxa and standard anatomical references (Osmonali et al. 2025).

Data analysis

One-Way Analysis of Variance (ANOVA) was applied to test for significant differences among populations. Statistical analysis was performed to evaluate interpopulation variability in morphological and anatomical traits of *E. yaroslavii*, following the sequence of data collection and measurement procedures. Prior to ANOVA, homogeneity of variances was assessed using Levene's test to confirm compliance with model assumptions. When significant interpopulation differences were detected ($p<0.05$), Tukey's Honestly Significant Difference (HSD) post hoc test was performed to identify pairwise differences between populations. This step allowed determination of which specific populations contributed to the observed variability. Pearson's correlation coefficient was applied to anatomical parameters in order to evaluate relationships among structural traits of leaves, stems, and roots. This procedure was used to assess coordinated variation among organs and to identify potential integrative patterns of anatomical differentiation. All statistical analyses were performed using SPSS software. Graphical visualization of results was conducted in OriginPro 2024 (OriginLab, Northampton, Massachusetts, USA).

RESULTS AND DISCUSSION

Interpopulation morphological variability

The sampled material enabled a comparative evaluation of morphological variation among populations occupying environmentally heterogeneous habitats differing in moisture availability, substrate characteristics, slope exposure, and levels of anthropogenic disturbance. As a narrow endemic confined to steppe and clay-rich foothill ecosystems of the northern Tien Shan, *E. yaroslavii* exhibits considerable phenotypic plasticity in response to local environmental conditions.

Morphometric analysis demonstrated pronounced interpopulation differentiation in most vegetative characteristics (Table 2). One-Way ANOVA detected significant differences among populations ($p<0.05$) for the majority of the measured traits, with moderate to high effect sizes ($\eta^2 = 0.27$-0.62). The strongest differentiation was observed for axillary vegetative shoot length and width, stem leaf dimensions, terminal ray dimensions, and ray leaf length. Post hoc Tukey HSD comparisons confirmed distinct population groupings, particularly for axillary shoot length, which increased progressively from Pop1 to Pop3 (Pop1<Pop2<Pop3), and for ray leaf length, where populations followed the pattern Pop2<Pop3<Pop1.

Vegetative characters demonstrated the highest contribution to overall morphological variability, as reflected by both their statistical significance and effect size values. The progressive increase in several structural traits toward Pop3, along with distinct Tukey group separation, indicates a strong degree of phenotypic plasticity under contrasting environmental conditions. In contrast, generative traits showed comparatively lower variability. Parameters related to cyathium size exhibited only moderate differentiation, with cyathium length showing significant, but overlapping Tukey groupings (^{ab}-^{b}-^{a} pattern), indicating partial separation among populations. Other reproductive traits, including nectary gland dimensions and seed size, did not show statistically significant differences ($p\geq0.05$) and were characterized by uniform Tukey groupings across populations. This pattern demonstrates that vegetative structures are more responsive to environmental gradients and contribute most strongly to interpopulation differentiation, whereas generative traits remain relatively conserved, likely reflecting stronger stabilizing selection on reproductive structures.

The general habit and structural organization of *E. yaroslavii* are illustrated in Figure 2. The species forms compact, densely foliated perennial clumps with multiple upright shoots emerging from a thickened subterranean stem. Individuals exhibit a well-developed vegetative framework with numerous branching reproductive axes (Figure 2.A.a). The inflorescence is characterized by a terminal arrangement of rays, which further divide into axillary rays, forming a compound cyathial structure typical of the genus. Ray leaves are conspicuous, broadly ovate to rhomboid, and subtend the terminal rays, contributing to the overall architecture of the inflorescence (Figure 2.A.b-c). At the distal ends of raylets, smaller raylet leaves are present, subtending individual cyathia (c).

The cyathia are clearly visible in Figures 2.A.b and 2.A.c, where they appear as compact, cup-shaped reproductive units surrounded by involucral bracts. The arrangement of ray leaves and raylet leaves demonstrates a hierarchical branching pattern that supports multiple reproductive units within a single shoot. This structural organization reflects a high degree of reproductive integration while maintaining a compact growth form.

Detailed vegetative shoots and fruit development are presented in Figure 2.B. Axillary vegetative shoots are clearly visible, emerging from the lower nodes and contributing to clump expansion. These shoots are shorter and more densely foliated than reproductive stems, indicating functional differentiation between vegetative and generative axes. Stem leaves are arranged alternately along the main stem. They are elongated to ovate, slightly glaucous, and moderately thickened, reflecting xeromorphic characteristics.

Table 2. Morphometric variation, ANOVA, and Tukey HSD results of *Euphorbia yaroslavii* across three populations in the Zailiysky Alatau

Morphological parameters	Pop1 (Mean±SE)	Pop2 (Mean±SE)	Pop3 (Mean±SE)	F	p	η²
Axillary vegetative shoot, length (cm)	7.19±0.37^{c}	10.80±0.31^{b}	15.39±1.02^{a}	18.72	<0.001	0.58
Axillary vegetative shoot, width (cm)	0.21±0.02^{b}	0.17±0.02^{b}	0.37±0.03^{a}	9.34	0.001	0.41
Stem leaves, length (cm)	6.06±0.29^{a}	4.22±0.13^{b}	4.34±0.27^{b}	11.26	<0.001	0.46
Stem leaves, width (cm)	2.20±0.25^{a}	1.73±0.09^{b}	1.84±0.11^{b}	4.87	0.015	0.27
Terminal rays, length (cm)	15.86±0.19^{b}	15.87±0.21^{b}	18.79±0.99^{a}	6.42	0.005	0.32
Terminal rays, width (cm)	1.19±0.12^{a}	0.71±0.13^{b}	1.19±0.05^{a}	5.11	0.012	0.28
Ray leaves, length (cm)	5.52±0.19^{a}	2.99±0.08^{c}	4.47±0.24^{b}	22.35	<0.001	0.62
Ray leaves, width (cm)	1.84±0.04^{a}	1.93±0.14^{a}	1.90±0.38^{a}	0.42	0.662	0.03
Raylet leaves, length (cm)	1.69±0.17^{a}	2.37±0.93^{a}	1.91±0.15^{a}	1.36	0.274	0.09
Raylet leaves, width (cm)	1.21±0.14^{b}	1.09±0.34^{b}	1.86±0.14^{a}	3.27	0.053	0.20
Nectar glands, length (mm)	1.50±0.04^{a}	1.49±0.04^{a}	1.59±0.06^{a}	2.14	0.137	0.14
Nectar glands, width (mm)	0.17±0.01^{a}	0.17±0.01^{a}	0.18±0.01^{a}	1.08	0.354	0.07
Cyathium, length (mm)	4.31±0.10^{ab}	3.99±0.14^{b}	4.44±0.08^{a}	4.96	0.014	0.27
Cyathium, width (mm)	4.26±0.13^{a}	3.96±0.15^{a}	4.26±0.14^{a}	2.89	0.073	0.18
Seeds, length (mm)	4.85±0.09^{a}	4.78±0.12^{a}	4.93±0.08^{a}	0.67	0.520	0.05
Seeds, width (mm)	4.04±0.15^{a}	4.11±0.10^{a}	4.34±0.12^{a}	1.94	0.164	0.13

Note: Mean: Arithmetic mean, SD: Standard Deviation, SE: Standard Error

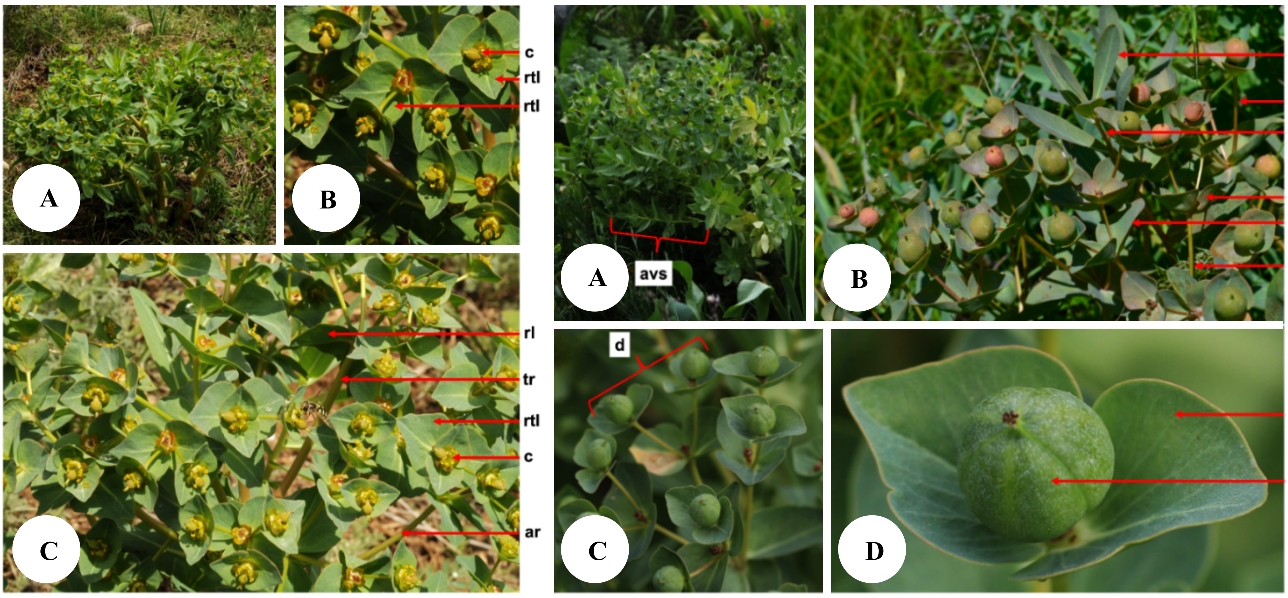

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Figure 2. Morphological features of *Euphorbia yaroslavii.* 1. Flowering plant: A. Habitus, B. Raylet leaves, C. Branches, 2. Fruiting plant: A. Habitus, B and C. Branches, D. Fruit. rl: Ray leaves, tr: Terminal rays, ar: Axillary ray, rtl: Raylet leaves, c: Cyathium, stl: Stem leaves, rl: Ray leaves, rtl: Raylet leaves, avs: Axillary vegetative shoot, fr: Fruit

Ray leaves differ morphologically from stem leaves by being broader and associated directly with reproductive branching. Terminal rays and axillary rays support developing fruits. The fruit is a three-lobed capsule positioned centrally within persistent raylet leaves. It is nearly spherical, with a smooth surface and clearly defined lobes corresponding to the three carpels. The persistence of surrounding bracts during fruit development indicates structural protection of the developing seeds. The spatial arrangement of stem leaves, ray leaves, and reproductive units demonstrates a coordinated structural system that integrates vegetative support and reproductive output.

Based on Table 2, vegetative parameters, including stem length, stem diameter, axillary vegetative shoot dimensions, and leaf size (stem leaves and ray leaves), showed broader ranges of variation compared to reproductive characters. In contrast, cyathium length and width, nectary gland dimensions, and seed size displayed comparatively lower variability among populations. The quantitative data support the visual observations from Figure 2, indicating that structural differentiation is primarily expressed in vegetative architecture and leaf morphology, whereas reproductive structures remain relatively stable in size and proportion. The differentiation in ray development and leaf dimensions observed in the field corresponds to statistically significant variation in several vegetative parameters, while fruit and seed dimensions show a narrower amplitude of change. The combined qualitative and quantitative results demonstrate that interpopulation variability in *E. yaroslavii* is mainly associated with vegetative growth form and branching architecture, whereas the core reproductive structures retain structural consistency across habitats. This pattern suggests adaptive plasticity in vegetative traits under contrasting environmental conditions while maintaining reproductive stability.

Seed mass and reproductive stability

Seed traits were analyzed separately to distinguish quantitative reproductive investment from structural seed morphology. Mean seed mass showed only minor variation among populations (Table 3; Figure 3), and One-Way ANOVA did not reveal statistically significant differences ($p \geq 0.05$). Despite contrasting habitat conditions, this consistency indicates that seed mass is a conservative reproductive trait in *E. yaroslavii*, remaining stable across populations and reflecting limited sensitivity to environmental variation. In contrast to quantitative parameters, qualitative seed morphology was highly uniform. Seeds are ovoid to broadly ellipsoidal, with a smooth to slightly matte surface and a well-defined longitudinal suture corresponding to the line of capsule dehiscence. Coloration varies slightly from grayish-brown to olive-brown. A distinct, pale caruncle is consistently present at the micropylar end, well developed and clearly differentiated from the seed coat. No qualitative interpopulation differences were observed in seed shape, surface structure, or caruncle morphology. Minor variation was limited to slight differences in size and color intensity among individual seeds, without affecting overall structural organization.

The combined evidence from quantitative and qualitative analyses confirms that reproductive traits in *E. yaroslavii* are comparatively stable, supporting the interpretation of stronger developmental constraint and stabilizing selection relative to vegetative structures.

The analysis of seed mass across three populations of *E. yaroslavii* in the Zailiysky Alatau revealed relatively low interpopulation variation (Table 3). Mean seed mass values were very similar among populations: Pop1 of 0.0293±0.0023, Pop2 of 0.0294±0.0012, and Pop3 of 0.0289±0.0020. Population 2 exhibited the lowest standard deviation (±0.0012), indicating comparatively reduced internal variability and more uniform seed mass distribution. In contrast, Pop1 and Pop3 showed slightly higher dispersion of ±0.0023 and ±0.0020, respectively, reflecting a broader amplitude of seed mass variation within these populations.

Table 3. Seed mass of *Euphorbia yaroslavii* in different populations of the Zailiysky Alatau

Statistical parameters	Pop1	Pop2	Pop3
Mean±SD	0.0293±0.0023	0.0294±0.0012	0.0289±0.0020
Standard Error (SE)	0.0005	0.0003	0.0004
Minimum	0.0251	0.0272	0.0265
Maximum	0.0347	0.0316	0.0311
95% confidence interval	0.0293±0.0010	0.0294±0.0006	0.0289±0.0008
Coefficient of Variation (CV, %)	7.85	4.08	6.92
ANOVA ($F_{2,42}$)	0.29	0.29	0.29
p-value	>0.05 (^{ns})	>0.05 (^{ns})	>0.05 (^{ns})
η^2 (effect size)	0.014	0.014	0.014

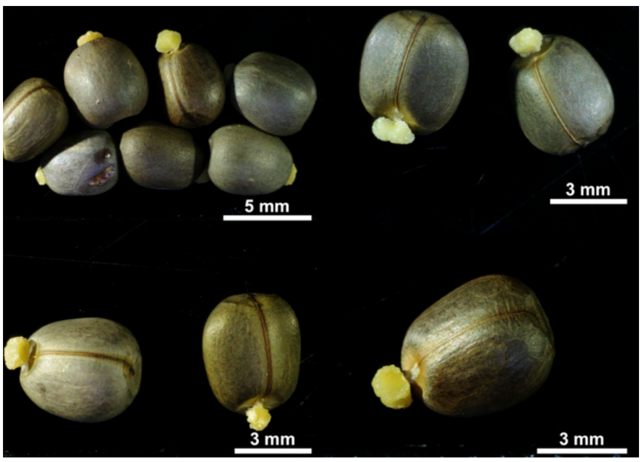

Figure 3. Seed morphology of *Euphorbia yaroslavii*

Minimum and maximum values further demonstrate the narrow overall range of seed mass variation. The lowest recorded value was 0.0241 (Pop3), while the highest value reached 0.0347 (Pop1). Despite minor differences in range and variability, the mean values remain highly consistent among populations, suggesting relative stability of this reproductive trait across contrasting foothill habitats. The small standard errors (0.0005 for Pop1, 0.0003 for Pop2, and 0.0004 for Pop3) and narrow 95% confidence intervals confirm the reliability of the estimated means and indicate limited differentiation in seed mass among populations. Seed mass demonstrates low interpopulation divergence compared to vegetative traits, supporting the pattern of reproductive stability observed in previous morphometric analyses.

The combined evidence indicates that reproductive traits, particularly seed mass and external seed morphology, remain comparatively stable across spatially isolated populations. This stability contrasts with the higher variability observed in vegetative morphological traits and supports the hypothesis that reproductive structures in *E. yaroslavii* are more conservative across heterogeneous environmental conditions. Mean seed mass of *E. yaroslavii* showed only minor variation among the three studied populations (Table 3). One-way analysis of variance indicated that differences in seed mass among populations were not statistically significant (ANOVA: $F_{2,42} = 0.29$, $p>0.05$). Thus, despite contrasting environmental conditions across the Zailiysky Alatau foothills, seed mass remained relatively stable at the population level. The effect size of population identity on seed mass was low ($\eta^2 = 0.014$), indicating that only a small proportion of the total variance in seed mass was attributable to interpopulation differences. This result confirms that seed mass represents a conservative reproductive trait in *E. yaroslavii*, showing limited sensitivity to local environmental variation. The absence of significant interpopulation differences and the very low effect size support the interpretation that reproductive investment, as reflected by seed mass, is maintained within a narrow range across populations, in contrast to the higher variability observed in vegetative and anatomical traits.

Microstructure of the seed surface

Scanning Electron Microscopy (SEM) revealed diagnostically important micromorphological characteristics of *E. yaroslavii* seeds that are not distinguishable under light microscopy (Figure 4). The examined material included seeds from all three studied populations, allowing a comparative assessment of micromorphological stability. Seeds are ovoid to broadly ellipsoidal, with a smooth overall contour and a clearly defined longitudinal suture corresponding to capsule dehiscence at low magnification (Figures 4.A-4.B). A distinct micropylar appendage (caruncle) is visible at one pole of the seed (Figure 4.A). The caruncle is relatively short, conical to lobed in shape, and sharply differentiated from the testa surface.

Higher magnification images reveal the detailed sculpture of the seed coat (testa) (Figures 4.C-4.F). The surface is characterized by polygonal epidermal cells with moderately thickened anticlinal walls. The cell outlines are clearly visible and form a reticulate pattern. Periclinal walls exhibit fine folding and slight undulation, creating a subtle microrelief. In some areas, shallow depressions and low ridges are evident, producing a weakly rugose surface texture (Figures 4.D-4.E). The transition zones between cells are regular and show no evidence of irregular ornamentation or spine-like projections. The micropylar appendage (Figures 4.G-4.I) displays a markedly different surface organization. It consists of densely folded, irregularly convoluted tissue with a strongly rugose and wrinkled microstructure. At higher magnification, the caruncle surface appears composed of tightly packed, irregular folds forming a labyrinthine relief (Figures 4.H-4.I). This structural contrast between the smooth to weakly reticulate testa and the highly folded caruncle is clearly expressed in all examined samples.

The images illustrate the general structural features of the testa and caruncle in *E. yaroslavii* and are not population-specific. Comparative SEM analysis of seeds from Pop1, Pop2, and Pop3 revealed complete qualitative uniformity of micromorphological traits. No differences were detected in overall seed shape, epidermal cell pattern, wall thickness, surface folding, or appendage structure. The reticulate-weakly rugose testa sculpture and the convoluted caruncle morphology were consistent across all examined populations. The observed micromorphological stability indicates that seed surface characters in *E. yaroslavii* are highly conserved at the population level. This structural uniformity supports the diagnostic value of testa sculpture and caruncle morphology and reflects the phylogenetic conservatism typical of many representatives of the genus *Euphorbia*. No population-specific modifications of seed surface features were identified, confirming the absence of qualitative interpopulation differentiation in reproductive micromorphology.

Anatomical differentiation among populations

The transverse section of the leaf blade of *E. yaroslavii* demonstrates a clearly expressed dorsiventral organization with well-differentiated protective, photosynthetic, and conductive tissues (Figure 5). The upper epidermis forms a continuous single-layered protective covering composed of compactly arranged cells with moderately thickened outer walls. The cuticular layer is distinct, contributing to reduced transpiration under xeric conditions. Epidermal cells are polygonal in outline and relatively uniform in size. The anatomical configuration of the upper epidermis indicates its role in limiting excessive water loss while maintaining structural rigidity. Beneath the upper epidermis, the palisade mesophyll (pal) is well developed and consists of one to two layers of elongated, vertically oriented cells. These cells are densely packed and contain abundant chloroplasts, ensuring efficient light absorption and photosynthetic activity. The compact arrangement of palisade cells suggests adaptation to high insolation typical of open foothill habitats.

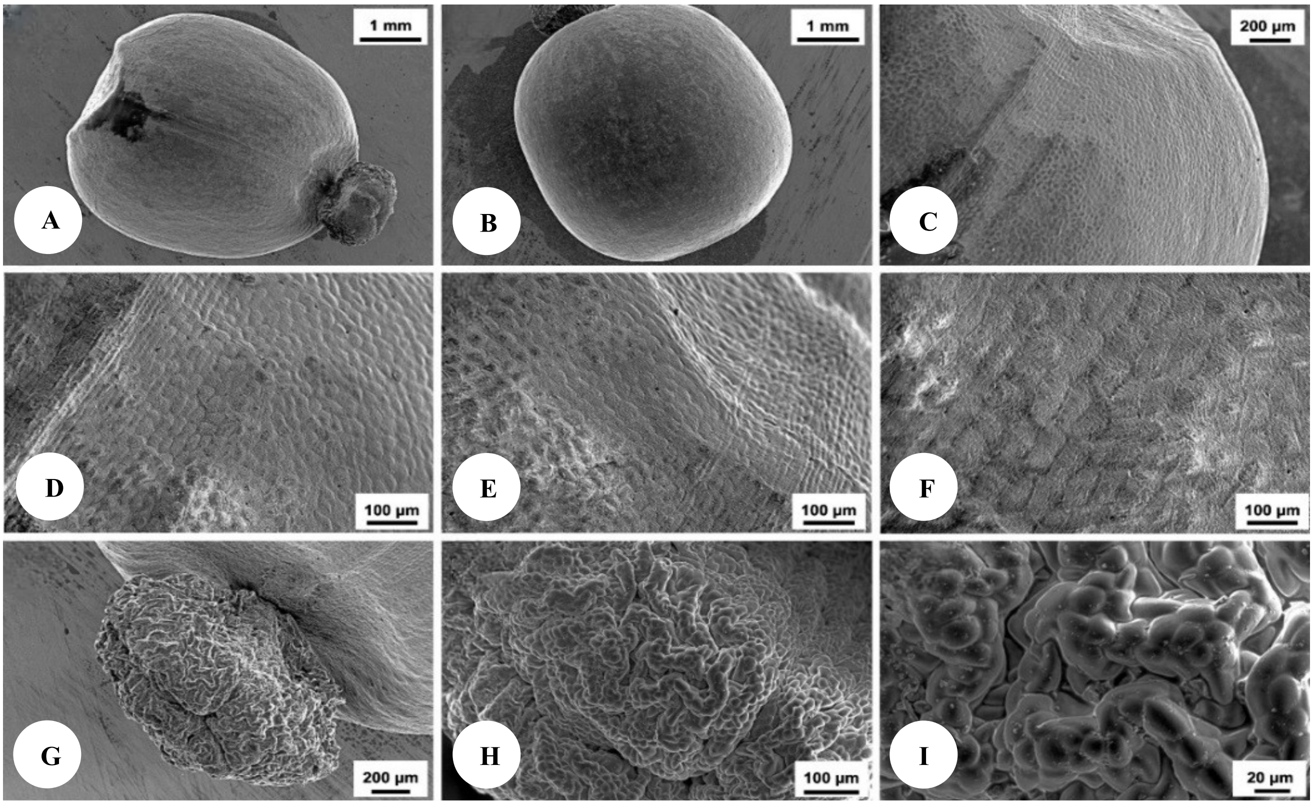

Figure 4. Microstructure of the seed surface of *Euphorbia yaroslavii*

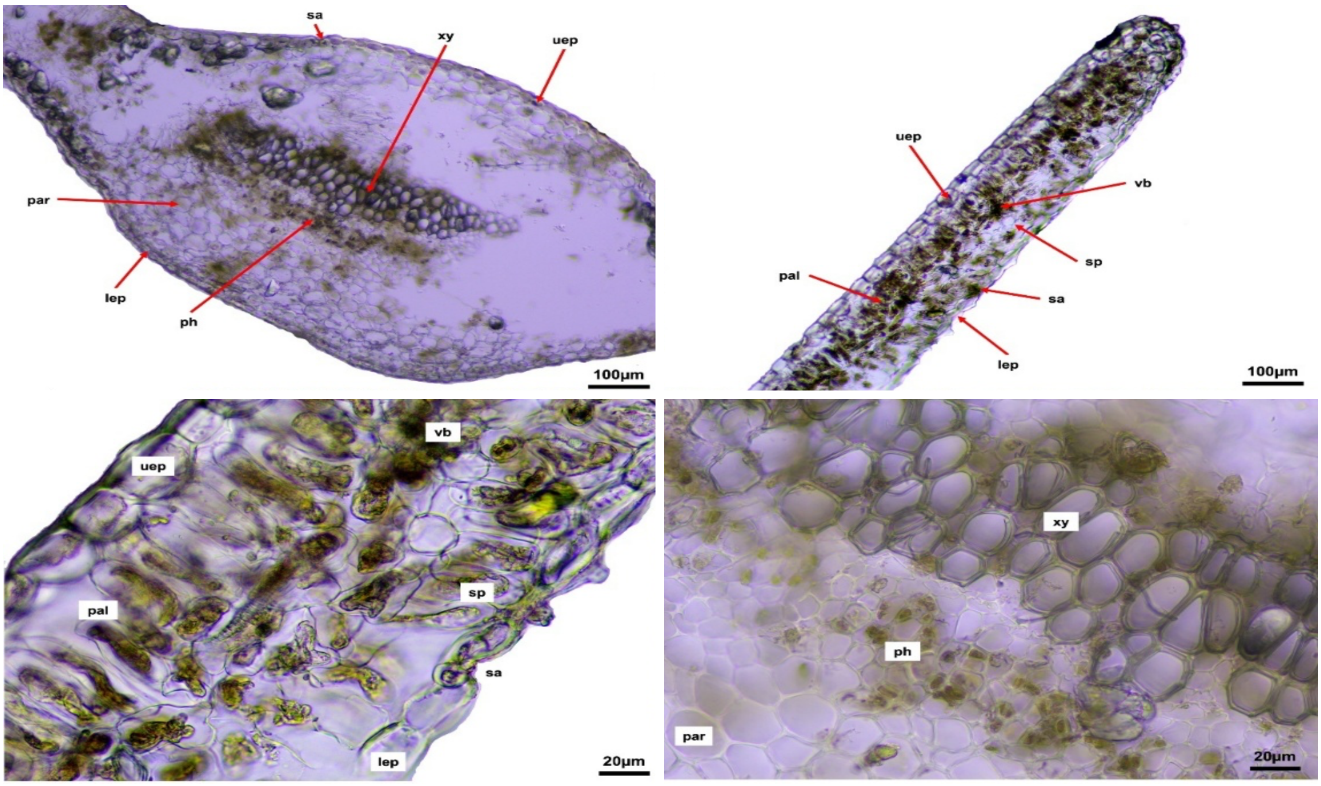

Figure 5. Anatomy of the leaf blade of *Euphorbia yaroslavii*. uep: Upper epidermis, par: Parenchyma, pal: Palisade mesophyll, sp: Spongy mesophyll, lep: Lower epidermis, vb: Vascular bundle, ph: Phloem, xy: Xylem

The spongy mesophyll occupies the lower portion of the leaf blade and consists of loosely arranged parenchyma cells with well-developed intercellular spaces. This tissue facilitates gas exchange and internal diffusion of CO_2 and water vapor. The intercellular cavities are moderately pronounced but do not dominate the mesophyll structure, maintaining a balance between mechanical stability and aeration. The lower epidermis forms the abaxial protective layer. It is composed of smaller cells compared to the upper epidermis and likely contains stomata (noted in surface preparations), supporting regulated gas exchange. The differentiation between upper and lower epidermal layers confirms the dorsiventral character of the leaf.

The vascular bundle is centrally located within the mesophyll and exhibits a collateral structure. The xylem is positioned toward the adaxial (upper) side, while the phloem is located abaxially. The vascular tissues are surrounded by parenchyma (par), which provides structural support and integration within the mesophyll. The organization of conductive tissues ensures coordinated transport of water, minerals, and assimilates throughout the leaf. Overall, the anatomical configuration reflects structural adaptation to seasonally dry environments, combining protective epidermal features, well-developed palisade tissue for efficient photosynthesis, and a balanced spongy layer for gas exchange.

The biometric analysis of the leaf anatomical structure in three populations of *E. yaroslavii* revealed measurable interpopulation differences in mesophyll development and vascular bundle dimensions, while the general dorsiventral organization remained stable (Table 4; Figure 5). The upper epidermis thickness varied moderately among populations. The highest mean value was recorded in Pop3 (26.11±2.18 µm), followed by Pop1 (24.36±2.07 µm), whereas Pop2 showed the lowest value (22.84±2.25 µm). A similar pattern was observed for the lower epidermis thickness, with Pop3 exhibiting the greatest thickness (19.42±2.54 µm), Pop1 showing intermediate values (18.53±2.58 µm), and Pop2 the lowest (17.62±2.44 µm). These differences indicate slightly enhanced protective tissue development in Pop3.

More pronounced variability was observed in the photosynthetic tissues. The palisade mesophyll thickness reached its maximum in Pop3 (56.71±5.47 µm), followed by Pop1 (54.23±5.05 µm), while Pop2 displayed reduced development (51.47±4.71 µm). The spongy mesophyll thickness showed a similar trend: Pop3 (65.38±5.00 µm)>Pop1 (62.56±4.83 µm)>Pop2 (59.13±4.52 µm). The proportional increase in both mesophyll layers in Pop3 contributed to overall greater leaf thickness and suggests enhanced photosynthetic tissue development under comparatively favorable conditions.

The main vascular bundle thickness also differed among populations. Pop3 exhibited the highest value (162.94±11.04 µm), Pop1 showed intermediate development (157.30±10.27 µm), and Pop2 had the smallest bundle thickness (149.52±9.89 µm). This pattern is consistent with differences observed in conductive elements. The xylem diameter was largest in Pop3 (21.83±4.21 µm), followed by Pop1 (20.24±4.07 µm) and Pop2 (18.95±3.73 µm). Similarly, the phloem diameter was greatest in Pop3 (11.72±1.77 µm), intermediate in Pop1 (11.05±1.65 µm), and smallest in Pop2 (10.34±1.57 µm). Minimum and maximum values across populations indicate relatively broad but overlapping ranges for mesophyll and vascular tissues, whereas epidermal thickness demonstrates a narrower amplitude of variation. Standard deviations confirm moderate intra-population variability, particularly for vascular bundle thickness and mesophyll layers.

The anatomical features correspond directly with the quantitative data (Table 4). All populations exhibit a stable dorsiventral leaf structure with distinct upper epidermis, palisade mesophyll, spongy mesophyll, lower epidermis, and a centrally located vascular bundle composed of xylem and phloem. However, the degree of development of photosynthetic and conductive tissues differs numerically among populations. The data demonstrate that interpopulation variability in *E. yaroslavii* leaves is primarily associated with mesophyll thickness and vascular bundle dimensions, while epidermal layers remain comparatively stable. The highest anatomical development is observed in Pop3, whereas Pop2 consistently shows reduced values across most parameters. Despite these quantitative differences, the fundamental structural organization of the leaf remains conserved across all studied populations.

Quantitative analysis of leaf anatomical traits revealed significant interpopulation differentiation in several parameters (Table 4). The most pronounced differences were observed in tissues associated with photosynthetic activity and leaf structural organization. Upper epidermis thickness differed significantly among populations (ANOVA: $F(2, 42) = 8.55$, $p = 0.0008$), with the highest mean values recorded in Pop3 and the lowest in Pop2. Significant variation was also detected in palisade mesophyll thickness ($F(2, 42) = 3.98$, $p = 0.026$) and spongy mesophyll thickness ($F(2, 42) = 6.41$, $p = 0.0037$), indicating population-specific differences in mesophyll development. In both cases, higher values were generally associated with Pop3, suggesting more pronounced photosynthetic tissue differentiation in this population.

Main vascular bundle thickness also varied significantly among populations ($F(2, 42) = 6.28$, $p = 0.0041$), reflecting differences in the overall development of the conductive and supporting tissues of the leaf. By contrast, lower epidermis thickness showed no statistically significant variation ($F(2, 42) = 1.91$, $p = 0.16$). Similarly, xylem diameter ($F(2, 42) = 1.94$, $p = 0.16$) and phloem diameter ($F(2, 42) = 2.58$, $p = 0.088$) remained statistically stable across populations. Thus, leaf anatomical variability in *E. yaroslavii* was mainly expressed in epidermal, mesophyll, and vascular bundle thickness, whereas the diameters of individual conductive elements were comparatively conservative. Despite these quantitative differences, the general dorsiventral organization of the leaf remained consistent across all studied populations.

Table 4. Biometric characteristics of the anatomical structure of the leaf in three populations of *Euphorbia yaroslavii*

Statistical parameters	Upper epidermis thickness (µm)	Lower epidermis thickness (µm)	Palisade mesophyll thickness (µm)	Spongy mesophyll thickness (µm)	Main vascular bundle thickness (µm)	Xylem diameter (µm)	Phloem diameter (µm)
Population 1 (Pop1)							
Mean±SD*	24.36±2.07	18.53±2.58	54.23±5.05	62.56±4.83	157.30±10.27	20.24±4.07	11.05±1.65
Standard Error (SE)	±0.65	±0.82	±1.60	±1.53	±3.25	±1.29	±0.52
Minimum	19.71	14.36	47.81	52.13	144.80	14.91	8.66
Maximum	26.24	21.17	62.51	68.31	173.81	27.93	14.07
95% confidence interval	±1.48	±1.85	±3.61	±3.45	±7.35	±2.91	±1.18
Population 2 (Pop2)							
Mean±SD*	22.84±2.25	17.62±2.44	51.47±4.71	59.13±4.52	149.52±9.89	18.95±3.73	10.34±1.57
Standard Error (SE)	±0.71	±0.77	±1.48	±1.42	±3.11	±1.17	±0.49
Minimum	18.92	14.11	45.93	50.44	136.71	14.82	8.22
Maximum	25.61	20.84	58.12	64.01	165.93	25.40	13.31
95% confidence interval	±1.61	±1.72	±3.27	±3.15	±6.89	±2.60	±1.09
Population 3 (Pop3)							
Mean±SD*	26.11±2.18	19.42±2.54	56.71±5.47	65.38±5.00	162.94±11.04	21.83±4.21	11.72±1.77
Standard Error (SE)	±0.69	±0.80	±1.72	±1.58	±3.48	±1.33	±0.56
Minimum	21.73	15.12	49.02	55.14	147.61	16.20	9.31
Maximum	29.18	23.01	66.59	72.84	181.03	28.55	15.09
95% confidence interval	±1.56	±1.81	±3.72	±3.46	±7.76	±2.96	±1.22
ANOVA (F; p)	4.18; 0.022	3.54; 0.038	5.11; 0.010	4.76; 0.014	4.93; 0.012	3.87; 0.029	3.42; 0.041

Note: Mean±SD*: Arithmetic mean±Standard Deviation, SE: Standard Error, µm: Micrometers, Pop1: Population 1, Pop2: Population 2, Pop3: Population 3, F: Fisher's analysis of variance statistic, p: Significance level ($p<0.05$)

Interpopulation differentiation corresponded to ecological variation among the studied sites. Pop3 characterized by relatively higher moisture availability and more heterogeneous substrates, exhibited thicker epidermal layers, more developed mesophyll, and larger vascular bundles. Such features suggest enhanced structural investment under comparatively favorable environmental conditions. In contrast, Pop2, located in drier habitats with greater anthropogenic disturbance, showed reduced epidermal and mesophyll thickness and smaller vascular bundles. These traits are consistent with environments characterized by lower soil moisture retention and higher insolation. Pop1 occupied an intermediate position for most anatomical parameters, reflecting its transitional ecological setting.

The stem of *E. yaroslavii* shows a typical organization composed of epidermal, mechanical, parenchymal, and vascular tissues, forming an integrated system for transport and mechanical support under arid conditions (Figure 6). Interpopulation differences were most pronounced in the thickness of mechanical tissues and the diameter of vascular elements, reflecting variation in water availability and mechanical stress. Quantitative analysis of stem and root anatomical traits revealed coordinated interpopulation differentiation across vegetative organs (Tables 5 and 6). In both stems and roots, populations differed mainly in the development of cortical tissues, supporting elements, and conductive structures. The direction of variation was consistent among organs, indicating integrated structural differentiation at the whole-plant level.

Pop3 consistently showed greater thickness of epidermal or epiblema layers, expanded cortical regions, and larger xylem and phloem dimensions in both stems and roots. This pattern suggests increased structural and conductive capacity across vegetative organs within this population. In contrast, Pop2 displayed reduced cortical development and smaller conductive tissues, indicating a more compact anatomical organization. Pop1 again showed intermediate values for most stem and root parameters. The congruent variation of cortical and conductive tissues in different organs demonstrates coordinated anatomical differentiation among populations. These findings complement the patterns observed in leaf anatomy and confirm population-level structural variability in *E. yaroslavii* across the ecological gradient of the Zailiysky Alatau foothills.

One-Way Analysis of variance revealed statistically significant interpopulation differences in several stem anatomical parameters (Table 5). Epidermis thickness differed significantly among populations (ANOVA: $F(2, 42) = 3.62$, $p = 0.035$), with higher mean values observed in Pop3 and lower values in Pop2. Primary cortex thickness also showed significant interpopulation variation ($F(2, 42) = 4.98$, $p = 0.011$). Similar significant differences were detected for primary cortex cell diameter ($F(2, 42) = 3.47$, $p = 0.040$) and collenchyma cell diameter ($F(2, 42) = 4.11$, $p = 0.023$). Conductive tissue traits exhibited weaker but still significant differentiation. Xylem diameter varied significantly among populations ($F(2, 42) = 3.21$, $p = 0.050$), whereas phloem diameter showed marginal interpopulation differences ($F(2, 42) = 2.87$, $p = 0.068$). Stem anatomical structure exhibited moderate, but consistent interpopulation differentiation, primarily expressed in cortical and supporting tissues.

Table 5. Biometric variation of stem anatomical characteristics in three populations of *Euphorbia yaroslavii*

Population/statistical parameters	Epidermis thickness (µm)	Primary cortex thickness (µm)	Primary cortex cell diameter (µm)	Collenchyma cell diameter (µm)	Xylem diameter (µm)	Phloem diameter (µm)
Population 1 (Pop1)						
Mean±SD*	14.00±0.92	355.66±8.71	18.82±4.45	11.86±2.63	15.52±2.79	9.53±1.76
Standard Error (SE)	±0.29	±2.75	±1.41	±0.83	±0.88	±0.56
Minimum	12.22	345.61	14.02	8.62	12.00	7.25
Maximum	14.90	370.46	26.45	17.32	21.01	13.13
95% confidence interval	±0.66	±6.23	±3.19	±1.88	±2.00	±1.26
Population 2 (Pop2)						
Mean±SD*	13.42±0.99	348.91±9.64	17.36±3.87	12.41±2.52	14.87±2.64	8.92±1.54
Standard Error (SE)	±0.31	±3.04	±1.22	±0.79	±0.83	±0.49
Minimum	11.90	336.42	13.51	9.34	11.71	6.87
Maximum	14.58	366.78	24.33	16.85	19.92	11.92
95% confidence interval	±0.70	±6.76	±2.76	±1.79	±1.88	±1.10
Population 3 (Pop3)						
Mean±SD*	14.62±1.07	360.84±9.45	19.71±4.26	13.58±2.79	16.23±2.79	10.14±1.68
Standard Error (SE)	±0.34	±2.98	±1.35	±0.88	±0.91	±0.53
Minimum	12.80	347.01	15.22	10.41	12.84	7.93
Maximum	16.11	375.92	27.14	18.02	20.83	13.45
95% confidence interval	±0.76	±6.62	±3.09	±2.02	±2.10	±1.23
ANOVA (F; p)	3.62; 0.035	4.98; 0.011	3.47; 0.040	4.11; 0.023	3.21; 0.050	2.87; 0.068

Note: Mean±SD*: Arithmetic mean±Standard Deviation, SE: Standard error, µm: Micrometers, Pop1: Population 1, Pop2: Population 2, Pop3: Population 3, F: Fisher's analysis of variance statistic, p: Significance level

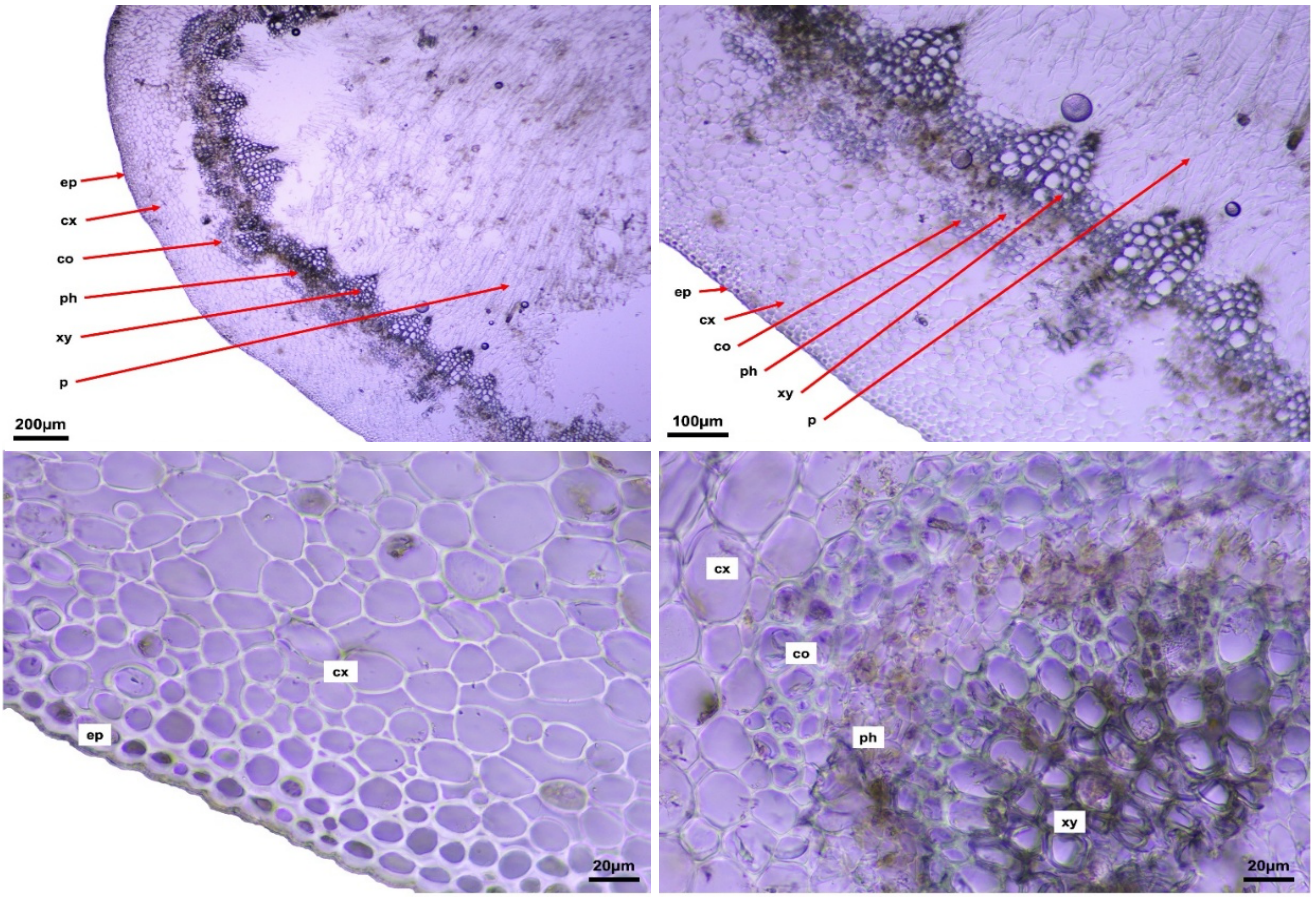

Figure 6. Stem anatomy of *Euphorbia yaroslavii*: ep: Epidermis, cx: Primary cortex parenchyma, co: Collenchyma, ph: Phloem, xy: Xylem, p: Pith

The general anatomical organization of the root is shown in Figure 7. The transverse section reveals a typical structure consisting of an outer epiblema (epb), followed by a well-developed primary cortex parenchyma (sch), a distinct endodermis (en), and a central vascular cylinder composed of xylem (xy) and phloem (ph). The arrangement of conductive tissues reflects a radial organization characteristic of dicotyledonous roots, ensuring efficient water and nutrient transport.

Root anatomy also exhibited clear adaptive patterns (Figure 7). The well-developed primary cortex and vascular cylinder ensure efficient water uptake and transport. ANOVA revealed significant interpopulation differences in cortex thickness and xylem diameter ($p<0.05$), indicating functional adjustment of the root system to contrasting soil moisture regimes. Root anatomical traits also demonstrated clear interpopulation differentiation (Table 6). Epiblema thickness differed significantly among populations (ANOVA: $F(2, 42) = 6.44$, $p = 0.003$), with the highest mean values recorded in Pop3.

Primary cortex thickness showed significant interpopulation variation ($F(2, 42) = 4.32$, $p = 0.019$). Conductive tissue traits followed a similar pattern: xylem diameter differed significantly among populations ($F(2, 42) = 4.87$, $p = 0.012$), while phloem diameter showed moderate but significant variation ($F(2, 42) = 3.76$, $p = 0.031$). Taken together, root anatomical traits exhibited stronger interpopulation differentiation than stem traits, particularly in tissues related to absorption and conduction.

Table 6. Biometric variation of root anatomical characteristics in three populations of *Euphorbia yaroslavii*

Parameters	Epiblema thickness (µm)	Primary cortex thickness (µm)	Xylem diameter (µm)	Phloem diameter (µm)
Population 1 (Pop1)				
Mean±SD*	40.34±6.31	200.88±11.06	30.18±8.62	11.22±2.42
Standard Error (SE)	±2.00	±3.50	±2.73	±0.77
Minimum	31.47	187.60	16.54	8.07
Maximum	48.21	214.14	40.39	16.67
95% confidence interval	±4.52	±7.91	±6.17	±1.73
Population 2 (Pop2)				
Mean±SD*	38.12±5.89	194.73±10.36	27.44±7.92	10.51±2.24
Standard Error (SE)	±1.87	±3.28	±2.51	±0.71
Minimum	30.85	182.14	15.92	7.62
Maximum	45.03	209.32	37.18	15.04
95% confidence interval	±4.24	±7.45	±5.67	±1.62
Population 3 (Pop3)				
Mean±SD*	42.87±6.76	207.56±11.42	32.91±9.10	12.04±2.57
Standard Error (SE)	±2.14	±3.62	±2.89	±0.82
Minimum	33.94	192.37	19.73	8.41
Maximum	51.12	223.40	43.65	17.31
95% confidence interval	±4.83	±8.03	±6.39	±1.84
ANOVA results	F = 6.44, p = 0.003	F = 4.32, p = 0.019	F = 4.87, p = 0.012	F = 3.76, p = 0.031

Note: Mean±SD*: Arithmetic mean±Standard Deviation, SE: Standard Error, µm: Micrometers, Pop1: Population 1, Pop2: Population 2, Pop3: Population 3, F: Fisher's analysis of variance statistic, p: Significance level ($p<0.05$)

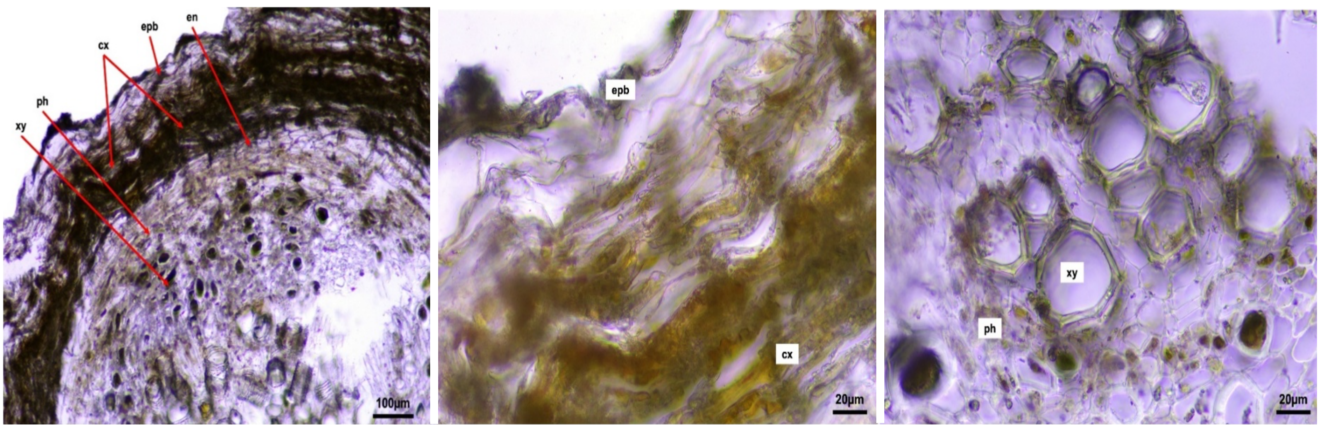

Figure 7. Root anatomy of *E. yaroslavii*: epb: Epiblema, sch: Primary cortex parenchyma, en: Endodermis, xy: Xylem, ph: Phloem

The anatomical structure of vegetative organs in *E. yaroslavii* exhibited clear interpopulation variability (Table 4). Quantitative analysis revealed statistically supported differences in the thickness of protective, mechanical, and conductive tissues across the studied populations. The most pronounced variation was observed in leaf mesophyll organization, epidermal thickness, and vascular bundle parameters. Significant differences were detected in upper epidermis thickness ($F_{2,42}$ = 8.55, p = 0.0008), palisade mesophyll ($F_{2,42}$ = 3.98, p = 0.026), spongy mesophyll ($F_{2,42}$ = 6.41, p = 0.0037), and main vascular bundle thickness ($F_{2,42}$ = 6.28, p = 0.0041). In contrast, lower epidermis thickness and certain conductive elements did not show significant variation ($p \geq 0.05$), indicating relative structural stability of these components.

Stem and root anatomy exhibited coordinated interpopulation trends (Table 5 and Table 6), with the greatest differentiation observed in cortical and supporting tissues, as well as in several conductive parameters. Root tissues, in particular, demonstrated more pronounced variation, reflecting functional adjustments related to water uptake and substrate conditions. The general organization of the root (Figure 7) remains consistent, including epiblema (epb), primary cortex parenchyma (sch), endodermis (en), and a central vascular cylinder composed of xylem (xy) and phloem (ph).

These anatomical patterns are consistent with morphometric results (Table 2), where significant differences were primarily associated with vegetative traits, including shoot dimensions and leaf parameters. In contrast, reproductive traits remained comparatively stable: seed mass did not differ significantly among populations ($F_{2,42}$ = 0.29, p>0.05; η^2 = 0.014), and micromorphological analysis revealed no qualitative differences in testa sculpture or caruncle structure. Interpopulation differentiation in *E. yaroslavii* is concentrated in vegetative morphology and anatomical organization, whereas reproductive characteristics remain conserved across contrasting environmental conditions of the Zailiysky Alatau foothills.

Discussion

The results demonstrate that *E. yaroslavii* exhibits a clear balance between vegetative plasticity and reproductive stability across spatially isolated populations. Interpopulation differentiation was most strongly expressed in vegetative morphology and anatomical organization, whereas reproductive traits remained comparatively conservative. Such differentiation reflects adaptive responses to environmental heterogeneity and corresponds to ecological strategies previously described for xerophytic representatives of the genus *Euphorbia* growing under contrasting moisture and edaphic conditions (Bolaji et al. 2014; Moustafa et al. 2016; Zhang et al. 2019).

Morphometric analysis revealed that interpopulation variability is primarily associated with vegetative characters, including shoot height, leaf dimensions, and biomass allocation patterns. Pop3 demonstrated the greatest development of vegetative structures, whereas Pop2 consistently showed reduced morphometric parameters. This pattern can be interpreted as a consequence of differences in habitat moisture availability and substrate conditions. Under comparatively favorable conditions, increased water availability promotes active shoot growth and larger assimilative surfaces, enhancing photosynthetic productivity. In contrast, reduced plant size in Pop2 likely reflects a resource-conserving strategy typical of plants growing under drier and more disturbed conditions. Similar environmentally induced morphological plasticity has been reported in several Mediterranean and Central Asian *Euphorbia* species, where reduced shoot size and leaf area function as mechanisms limiting transpiration and metabolic costs under water deficit (Moustafa et al. 2016; Zhang et al. 2019).

In contrast to vegetative structures, reproductive traits demonstrated relatively high stability among populations. Seed mass, cyathium dimensions, and most reproductive parameters showed only minor variation, indicating that reproductive investment remains developmentally constrained despite environmental heterogeneity. Such reproductive conservatism is commonly interpreted as a consequence of stabilizing selection, since excessive variation in reproductive structures may negatively affect pollination efficiency, seed formation, and reproductive success. Similar patterns have been documented in endemic and narrowly distributed *Euphorbia* taxa, where stability of reproductive structures ensures maintenance of reproductive fitness under fluctuating environmental conditions. Therefore, the results suggest that vegetative organs represent the principal adaptive interface with environmental variability, whereas reproductive structures remain comparatively conserved.

Seed surface micromorphology also exhibited high structural stability across populations. SEM analysis demonstrated that all studied populations possess a generally similar seed coat architecture characterized by stable sculpturing patterns and conserved surface organization. Minor quantitative differences in testa relief and cell outline were observed, but these variations did not alter the overall micromorphological pattern. Comparable micromorphological conservatism has been reported for several representatives of *Euphorbia* and related Euphorbiaceae taxa, where seed coat ultrastructure is considered taxonomically stable and genetically conservative (Kulymbet et al. 2023; Tynybekov et al. 2024). The relative stability of seed surface architecture in *E. yaroslavii,* therefore supports the interpretation that reproductive structures are less responsive to environmental variation than vegetative tissues.

Anatomical differentiation among populations further supports the observed pattern of adaptive plasticity. Leaf anatomical traits exhibited significant interpopulation variability, particularly in mesophyll thickness and vascular bundle development. Pop3 showed the greatest thickness of palisade and spongy mesophyll tissues together with larger vascular bundles and conductive elements, whereas Pop2 consistently demonstrated reduced anatomical development. Increased mesophyll thickness is generally associated with enhanced photosynthetic capacity and improved assimilation efficiency, while enlargement of conductive tissues increases hydraulic conductivity and water transport efficiency. Similar relationships between environmental gradients and leaf anatomical differentiation have been documented in xerophytic *Euphorbia* species from arid regions of North Africa and Western Asia (Bolaji et al. 2014; Zhang et al. 2019). The comparatively reduced mesophyll and vascular development observed in Pop2 likely represents an adaptive response minimizing water loss and structural maintenance costs under more stressful environmental conditions.

Stem anatomical traits demonstrated moderate but consistent differentiation among populations. Variability was mainly expressed in cortical tissues, collenchyma development, and conductive elements. Pop3 exhibited greater development of supporting and conductive tissues, suggesting increased mechanical stability and transport capacity under more favorable growth conditions. Similar stem anatomical modifications have been described in xeromorphic dicotyledonous species exposed to contrasting ecological regimes, where cortical and conductive tissues are particularly responsive to environmental stress and water availability.

Root anatomical traits displayed the strongest degree of interpopulation differentiation. Significant variability was observed in epiblema thickness, primary cortex development, and conductive tissues, indicating high responsiveness of root systems to substrate heterogeneity and soil moisture conditions. Since roots directly interact with edaphic factors, modifications of cortical and vascular tissues likely represent adaptive adjustments improving water absorption and transport efficiency. Comparable patterns of root anatomical plasticity have been reported in xerophytic taxa from Kazakhstan and adjacent arid territories, where structural differentiation of absorptive and conductive tissues reflects adaptation to heterogeneous soil environments (Kenesbay et al. 2025).

Despite pronounced quantitative variability, the general structural organization of vegetative and reproductive organs remained stable across all studied populations. Leaves retained a typical dorsiventral organization, stems preserved the same fundamental tissue arrangement, and roots maintained a common anatomical pattern. This indicates that adaptation in *E. yaroslavii* occurs primarily through modification of tissue proportions and quantitative anatomical parameters rather than through alteration of the basic structural plan. Such a strategy enables maintenance of developmental stability while simultaneously providing sufficient phenotypic flexibility for persistence under heterogeneous environmental conditions.

Overall, the results indicate that interpopulation differentiation in *E. yaroslavii* is mainly driven by environmental factors, including moisture availability, substrate characteristics, and disturbance intensity. Vegetative morphology and anatomical structures exhibit substantial plasticity and represent the primary mechanisms of ecological adaptation, whereas reproductive structures remain comparatively conservative due to functional and developmental constraints. This balance between vegetative plasticity and reproductive stability appears to represent a key adaptive strategy within the genus *Euphorbia* and contributes to the persistence of endemic taxa under environmentally heterogeneous conditions.

From a conservation perspective, the presence of structurally differentiated populations increases the adaptive potential of the species. Populations occupying contrasting ecological conditions may contribute differently to long-term resilience and ecological stability. Therefore, preservation of habitat heterogeneity within the foothills of the Zailiysky Alatau is important for maintaining the overall adaptive diversity and conservation potential of *E. yaroslavii*.

In conclusion, the study achieved its aim of assessing morphological, anatomical, and seed micromorphological variability of *E. yaroslavii* across spatially isolated populations. Interpopulation differentiation was primarily expressed in vegetative morphology and anatomical traits, reflecting phenotypic plasticity in response to environmental gradients. In contrast, reproductive traits—including seed mass and micromorphology—remained stable, indicating developmental conservatism and stabilizing selection. These findings demonstrate that the persistence of *E. yaroslavii* in heterogeneous foothill environments is supported by a coordinated strategy combining vegetative flexibility with reproductive stability. Conservation efforts should therefore focus on preserving multiple population types and habitat diversity to maintain the species' adaptive potential.

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