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Phenotypic variation in leaf and acorn traits in natural populations of *Quercus petraea*

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Abstract: Background *Quercus petraea* (Matt.) Liebl. holds significant ecological and economic value, yet phenotypic variation within its natural populations remains only partially explored. The main objectives of the study were: (1) to quantify the phenotypic variation in the analyzed leaf and acorn traits; (2) to determine the proportion of phenotypic variation occurring among and within populations; (3) to examine the pattern of population-level variation and its relationship with bioclimatic factors. Material and methods A total of 13 leaf traits and 10 acorn traits were analyzed in 64 sampled trees from seven natural populations. Descriptive statistics and population differentiation coefficients were calculated. The significance of differences in traits mean among populations and among trees within populations were assessed. Principal component analysis (PCA) was conducted at both the tree and population levels. Correlations between morphological principal components and bioclimatic variables were examined, and regression models were developed to evaluate relationships between significantly correlated morphological traits and bioclimatic factors. Results The coefficients of variation for the 23 traits ranged widely, from 12.08% for cupule width to 36.61% for petiole length, with an average of 20.36%. Nested ANOVA revealed substantial phenotypic variations both within and among populations. The primary source of variation was at the intra-population level, accounting for an average of 68.25%, which exceeded the inter-population variation (30.34%). The analyzed traits were reduced to six principal components, which together explained 88% of the phenotypic variation among trees. A statistically significant correlation between morphological principal components and bioclimatic variables was found for the first component, specifically with temperature related variables. Conclusions The study confirms that *Q. petraea* in Bosnia and Herzegovina exhibits considerable morphological variability, primarily within populations, and that leaf traits are strongly influenced by climatic gradients. Conservation strategies should prioritize the preservation of population integrity and patterns of local adaptation patterns, particularly in ecologically marginal or historically disturbed sites.

Keywords: *Quercus petraea*, natural population, variability, morphological traits

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Introduction

Sessile oak (*Quercus petraea* (Matt.) Liebl.) is a large, long-lived, deciduous broadleaved tree native to most of Europe. In Bosnia and Herzegovina, it occupies approximately 15% of all forests (Matić et al., 1971). Individuals can surpass 1,000 years in age and reach over 40 meters in height and 3–4 m in diameter (Colin Prentice & Helmisaari, 1991; Praciak, 2013; Eaton et al., 2016). Historically, sessile and pedunculate oaks played an important role in the development of societies in Europe by providing firewood, fruit for cattle feed, bark for tanning, and wood for construction (Eaton et al., 2016). However, their distribution was significantly reduced by anthropogenic pressure (Ducousso & Bordács, 2004). These included intensive and often unsustainable timber harvesting, widespread deforestation to clear land for agriculture, overgrazing by domestic animals which hindered natural regeneration, and the transformation of natural woodlands into managed forests dominated by faster growing, commercially valuable conifer species (Eaton et al., 2016).

Today, sessile oak populations face pressing conservation challenges, including restricted availability of suitable local seed sources, especially in marginal and edge populations, habitat instability, marked by the neglect of traditional woodland management systems (like coppice or acorn-use ecotypes) and their replacement by high-forest regimes, continuing human pressures, including the introduction of exotic genotypes, conversion to plantation forestry, and limited natural regeneration – all of which compromise genetic diversity and adaptive potential (Ducousso & Bordács, 2004).

Phenotypic variation in plants results from the combined effects of genetic factors and environmental influences accumulated over long periods of evolution (Miljković et al., 2019). The extent of phenotypic variation can reflect the genetic diversity within the studied material (Wang et al., 2023). Therefore, phenotyping traits is a fundamental method for assessing and researching the genetic diversity of forest tree resources, which is essential for their management and conservation (Wang et al., 2023). Given the historical reduction of sessile oak populations in Bosnia and Herzegovina (Begović, 1978), understanding phenotypic variation becomes even more crucial for conservation and adaptive management.

Phenotypic variation serves as a crucial adaptive mechanism (Edelaar et al., 2017; Liu et al., 2022), making it a central subject in studies of plant evolution, environmental adaptation, and conservation. Understanding trait variability – that is, the range of phenotypic differences in characteristics such as leaf size, thickness, seed and fruit dimensions – among sessile oak individuals and population is especially valuable. These differences, driven by both genetic variation and environmental response, enable selection for desirable traits. For instance, traits with high variability (like leaf thickness) highlight potential targets for genetic improvement, while more stable traits (such as seed dimensions) can guide reliable selection (as seen in *Eucommia ulmoides;* Wang et al., 2023). Clarifying these patterns supports better-informed breeding programs and sustainable management approaches by targeting the right traits for conservation and adaptation.

Numerous studies have demonstrated both intra- and inter-population variability in *Quercus petraea* across Europe, particularly in morphological traits such as leaf shape, size, and lobation, as well as genetic characteristics. Early work by Bruschi et al. (2003a; 2003b) in Italy documented extensive phenotypic variation both within individual trees and among different trees, which was largely attributed to environmental factors and positional effects influencing trait expression. These findings have been further supported by morphological and genetic studies conducted in Central and Southeastern Europe (e.g., Gömöry et al., 2001; Ballian et al., 2007; Rebrean et al., 2013; Tóth et al., 2023), including work specific to Bosnia and Herzegovina (Ballian & Bogunić, 2012; Ballian, 2016; Memišević Hodžić et al., 2024a).

More recent studies have broadened both the geographic and methodological scope of research in *Quercus petraea*. Yücedağ and Gailinig (2013) and Yücedağ et al. (2019, 2021) investigated morphological and genetic differentiation in Turkish populations. Kremer et al. (2002) reported stable morphological differences between *Quercus petraea* and *Quercus robur* across Western Europe, while Jurkšienė and Baliuckas (2014) found similar trends in Lithuanian populations. In Italy, Fortini et al. (2025) and Proietti et al. (2021) applied geometric morphometrics to assess intraspecific variation in sessile oak and related taxa. These studies collectively highlight the widespread and complex nature of phenotypic variation in *Q. petraea*, shaped by both genetic differentiation and environmental gradients. Taxonomic delimitation of *Q. petraea* populations in the Balkans is also a significant consideration. The region includes taxa historically identified as *Q. dalechampii* Ten. or *O. polycarpa* Shur (sensu Balkan authors), raising questions about species delimitation. While the typification of *Q. dalechampii* and its assignment to the collective group of *Q. pubescens* (Di Pietro et al., 2012) have clarified some taxonomic aspects, a debate is still open on which binomial should be applied to include the records of the oak material belonging to the *Q. petraea* group and previously classified (especially in Eastern Europe) as *Q. daleshampii* Ten. (Raab-Straube & Raus, 2013; Kučera, 2018; Kaplan et al., 2022). These taxa exhibit overlapping morphological traits, such as leaf shape and size, as well as similar ecological preferences. This overlap warrants careful interpretation of variation patterns, taking into account the specific characteristics of local floras and the regions' biogeographic history, to avoid misidentification or taxonomic confusion.

Phenotypic studies of sessile oak in Bosnia and Herzegovina remain limited. While the study by Memišević Hodžić et al. (2024a) offered detailed insights into leaf morphological variation among natural populations, comprehensive research incorporating additional traits and environmental variables is still needed.

Building on this foundation, the present study investigates phenotypic variation in *Quercus petraea* populations from Bosnia and Herzegovina. This study aims to quantify phenotypic variation in selected leaf and acorn traits, assess how this variation is distributed within and among populations, and explore the relationships between population-level phenotypic variation and bioclimatic factors. The results are expected to provide valuable insights that can inform genetic improvement programs, guide silvicultural practices, and promote the sustainable management of sessile oak forests by identifying key traits and environmental drivers influencing population variability.

Based on current knowledge and observed variability in morphological traits of *Quercus petraea*, we hypothesize that: Significant phenotypic variation exists both within and among natural populations of *Q. petraea* in Bosnia and Herzegovina, with greater within-population variation expected due to microenvironmental heterogeneity and high phenotypic plasticity of individuals. Populations located in different bioclimatic regions will exhibit distinct phenotypic profiles, particularly in leaf morphology and acorn traits, reflecting local adaptation to climatic factors.

Material and methods

Material

Plant material was collected during 2023 from eight to ten trees per population in seven natural populations in Bosnia and Herzegovina (Fig. 1, Table 1). Geographic coordinates of the sampling sites were recorded using GPS. Bioclimatic data were obtained from the WorldClim database (version 2.1), with the specific climate variables used in the analysis listed in Table 1.

Leaves were sampled only from short shoots on the outer, sunlit part of the crowns of mature, isolated trees or trees positioned at forest edges, an approach shown in previous studies to be appropriate for morphometric analysis and representative of population-level variation. This sampling strategy helps minimize seasonal and ontogenetic differences among individuals. From each tree, thirty leaves and thirty fruits were collected, transported to the laboratory, and subsequently pressed and fully dried for morphometric analysis. Specimens were identified as *Quercus petraea* based on expert knowledge in accordance with regional floristic expertise. Voucher specimens were prepared by pressing and drying

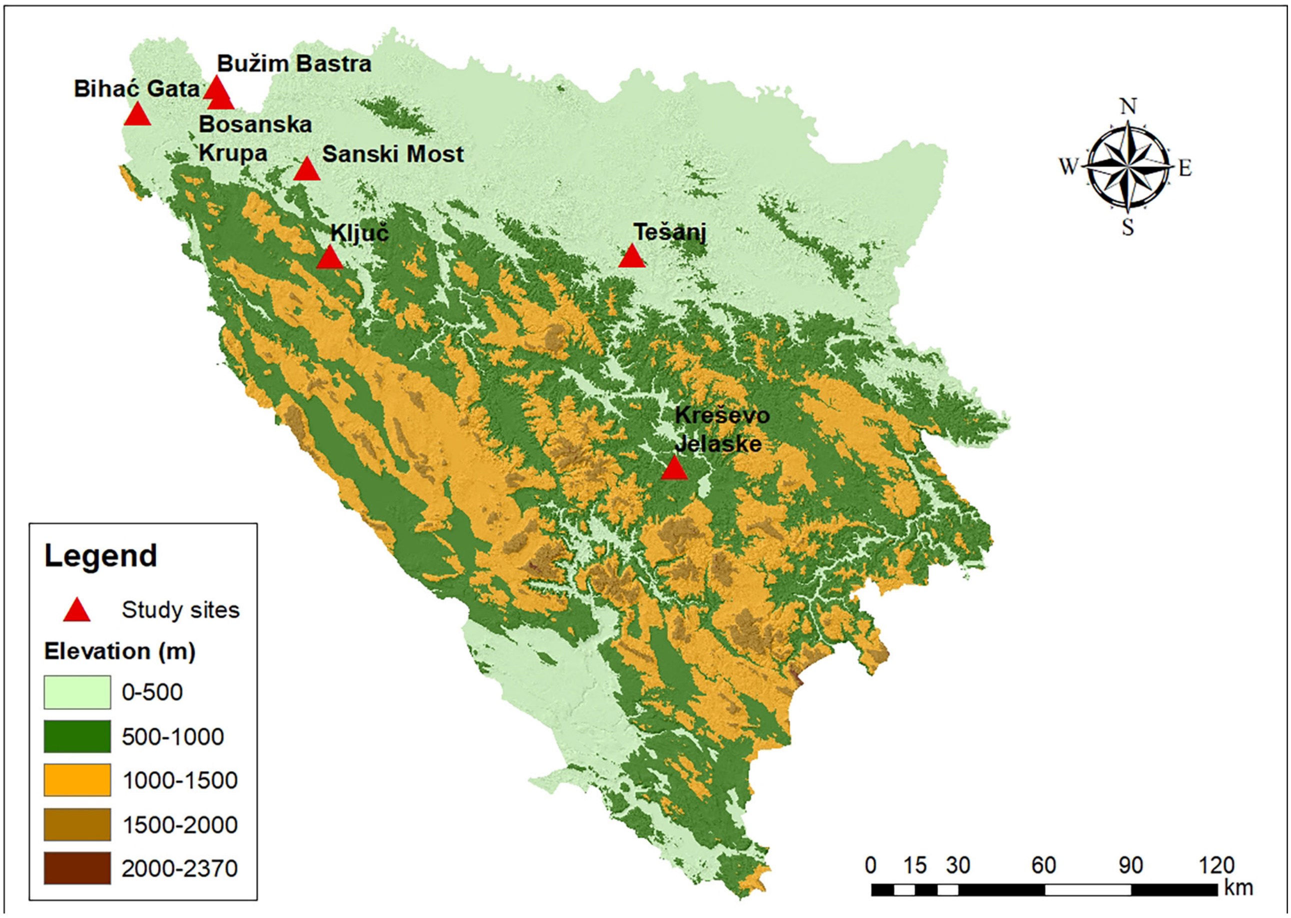

Fig. 1. Geographic locations of the investigated *Quercus petraea* populations

Table 1. Geographic locations and mean values of climatic variables for the investigated natural *Q. petraea* populations

No	Locality	Sample size	Longitude	Latitude	BIO1 (°C)	BIO05 (°C)	BIO09 (°C)	BIO10 (°C)	BIO11 (°C)
1.	Bihać Gata	8	15.81	44.99	10.65	26.49	2.97	19.31	1.51
2.	Bosanska Krupa	10	16.18	45.05	10.36	25.53	2.86	18.91	1.39
3.	Bužim Baštra	9	16.15	45.08	9.51	24.47	2.07	18.01	0.69
4.	Ključ	8	16.67	44.56	9.10	24.23	1.52	17.51	0.27
5.	Kreševo Jelaške	9	18.17	43.91	9.00	24.74	1.63	17.61	0.09
6.	Sanski Most	10	16.56	44.83	10.08	25.40	2.48	18.67	1.03
7.	Tešanj	10	17.74	44.65	9.41	25.58	1.88	18.27	0.15
Total		64			9.73	25.21	2.20	18.33	0.73

BIO1: Annual Mean Temperature, BIO05: Max Temperature of Warmest Month, BIO09: Mean Temperature of Driest Quarter, BIO10: Mean Temperature of Warmest Quarter, BIO11: Mean Temperature of Coldest Quarter.

leaves, while acorns were dried without pressing. All specimens were deposited in the collection at the University of Sarajevo – Faculty of Forestry.

Morphometric analysis

Dry leaves and acorns were measured using a digital caliper with an accuracy of 1 mm. Six phenotypic traits of leaves were directly measured (Fig. 2a), four additional traits were derived, and two were visually assessed (Fig. 2b). Similarly, six morphological traits of the acorn and cupule were measured (Fig. 2c), and four additional traits were derived.

Statistical analysis

Statistical analyses were performed on 23 phenotypic traits, based on three data levels: all individual data (1694 leaves and 1694 acorns), tree means (mean for 64 trees), and population means (means for seven populations).

Descriptive statistics. Descriptive statistics (maximum, minimum, mean value, standard deviation) were calculated for 23 phenotypic traits to assess phenotypic variation using the full dataset (1694 leaves and 1694 acorns). The coefficient of variation (CV) was also derived using the formula:

$$CV = (\text{standard deviation} \times 100) / \text{mean value}.$$

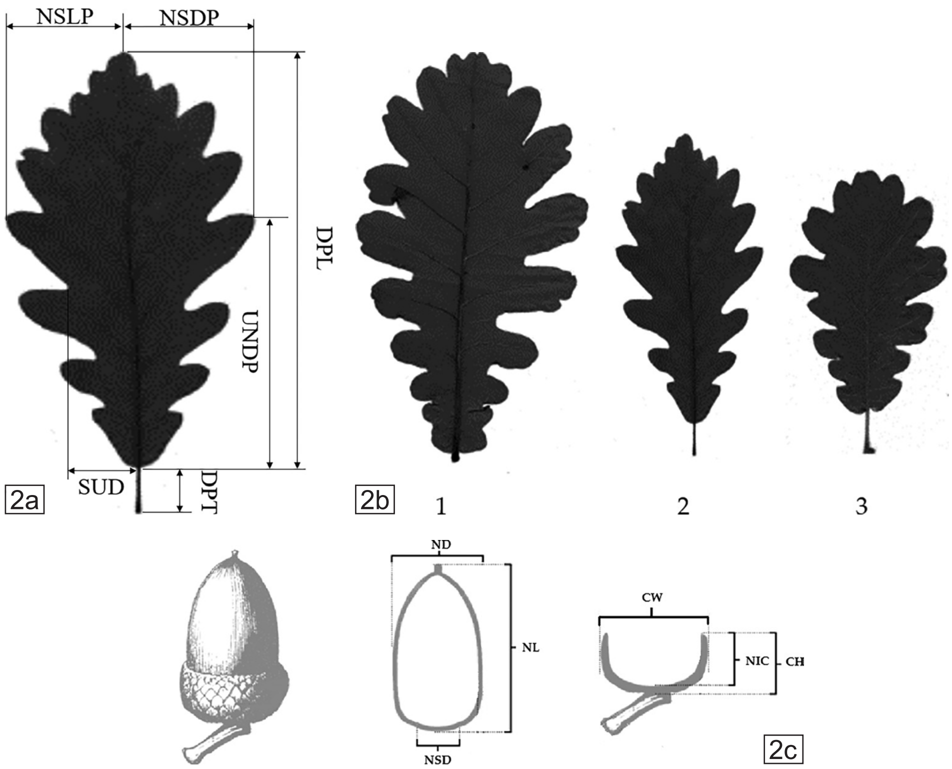

Fig. 2. Measured traits of leaves (2a); assessed trait of leaf base shape (2b) (Fortini et al., 2015); measured traits of the acorn and cupule (2c)

Table 2. List of measured, derived and assessed traits of leaves and acorns

Trait acronym	Trait name	Trait description	Unit	Type
LL	Leaf length	–	mm	Measured
PL	Petiole length	–	mm	Measured
WPD	Right-side base-to-widest-point distance	–	mm	Measured
RW	Right half-leaf maximum width	–	mm	Measured
LW	Left half-leaf maximum width	–	mm	Measured
LIW	Incision width below maximum width on the left side	–	mm	Measured
TLL	Total leaf length	Petiole length + leaf length	mm	Derived
TLW	Total leaf width	Left half-leaf width + right half-leaf width	mm	Derived
LW/LL	Leaf width to length ratio	–	–	Derived
PL/LL	Petiole length to leaf length ratio	–	–	Derived
LN	Number of lobes on the right side	–	–	Counted
LH	Leaf hairiness	1 – none, 2 – in the axils, 3 – on the entire leaf, 4 – along the central nerve	Categories (1,2,3,4)	Assessed
LBS	Leaf base shape	According to a predefined morphological scheme (Fig. 2b)	Categories (1,2,3)	Assessed
NL	Nut length	–	mm	Measured
ND	Nut diameter	–	mm	Measured
NSD	Nut scar diameter	–	mm	Measured
CW	Cupule width	–	mm	Measured
CH	Cupule height	–	mm	Measured
NIC	Nut in cupule	Cupule depth	mm	Measured
NL/ND	Nut length to nut diameter ratio	–	–	Derived
ND/NL	Nut diameter to nut length ratio	–	–	Derived
CW/CH	Cupule width to cupule length ratio	–	–	Derived
CH/CW	Cupule height to cupule width ratio	–	–	Derived

Analysis of variance (ANOVA). Population differentiation coefficients were calculated as the ratio of the variance between populations and the sum of variances between and within populations, multiplied by 100 (%) (Wang et al., 2023).

$$V_{st} = \frac{\sigma_i^2}{\sigma_i^2 + \sigma_{j(i)}^2} \times 100\%$$

where σ_i^2 represents the variance between populations and $\sigma_{j(i)}^2$ represents the variance within populations.

Variances were obtained using a nested ANOVA method, with two factors nested within the population factor. The nested ANOVA method followed linear model:

$$Y_{ijk} = \mu + \alpha_i + \beta_{j(i)} + e_{(ij)k}$$

where Y_{ijk} is the value of the kth observation value of the jth tree in the ith population, μ is the overall mean, α_i is the random effect of the ith population, $\beta_{j(i)}$ is the random effectof the jth tree in the ith population, and is the residual error (within-tree variation) of the ijk^{th} observation (Wang et al., 2023).

Variance Component Analysis (VCA). The proportions of variance components: among populations, among trees within populations, and within trees (error), for each trait, were estimated using the VCA package in R (Schuetzenmeister & Dufey, 2024). The significance of mean differences in traits among populations and among trees within populations was assessed using nested ANOVA, implemented with the "dplyr" (Wickham et al., 2025) and "broom" (Robinson et al., 2025) packages in R version 4.4.2.

Correlation analysis – tree level. To investigate the correlation between phenotypic traits at the tree level, correlation analysis was performed. Tree means of the 23 traits were standardized using Z-scores, and Pearson correlation coefficients were calculated. Correlations and their statistical significance were assessed using the "cor.test" function in R version 4.4.2 (R Core Team, 2025).

Principal component analysis (PCA) – the tree level. Principal component analysis (PCA) was used to evaluate phenotypic traits at the tree level and to identify those that differentiate among the sessile oak populations. The PCA was performed using a correlation matrix based on standardized tree means for 23 phenotypic traits. The main principal components are displayed in a biplot to analyse relations among trait groups (leaf, cupula and nut) and among *Quercus petraea* populations. These principal components were also used to visualize overall phenotypic variability between populations. The PCA was conducted using the "MorphTools2" package in R Version 4.4.2 (Šlenker et al., 2022).

Cluster analysis – the population level. Cluster analysis was used to examine the relationships among sessile oak populations. Population means for 23 traits were standardized and used in a clustering. Hierarchical clustering was performed using the unweighted pair group method with arithmetic mean (UPGMA) based on Euclidean distances, following the approach described by Koutecký (2015). In addition, Manhattan and Minkowski distance metrics, more suitable for high-dimensional space, were applied using the "MorphoTools2" (Šlenker et al., 2022). The resulting hierarchical clustering was visualized as a dendrogram using the „ggdendro"package in R (de Vries & Ripley, 2024).

Regression analysis – the population level. To examine relationships between morphological traits and climatic factors, principal components derived from population means of 23 phenotypical traits were related to bioclimatic variables presented in Table 1. The contributions of individual phenotypic traits to the principal components were evaluated to identify the main morphological features driving population differentiation. Relationships between these principal components (representing key morphological patterns) and bioclimatic variables were first assessed using a correlation matrix with Pearson's coefficients. Correlations between principal components and bioclimatic variables were interpreted to explore potential environmental influences. Finally, stepwise linear regression was applied to the principal components and bioclimatic variables to identify the most influential climatic factors affecting the main morphological traits of sessile oak leaves and acorns.

Results

Phenotypic variation of traits

Table 3 presents the results of the statistical analysis. The coefficient of variation (CV) for all measured traits ranged from 12.08% for cupule width to 36.61% for petiole length, with an overall mean CV of 20.36%. The average CV of leaf traits was 21.51%, while for the acorn traits it was 18.98%.

Phenotypic variation among and within populations

The analysis of variance components revealed distinct patterns of trait variability at three hierarchical levels: among populations, among trees within populations, and within trees (residual variation). On average, most of the variation was found within trees (mean = 51.84%), followed by among trees within populations (mean = 39.51%), while the smallest proportion of variance occurred among populations (mean = 8.64%) (Table 4). Some traits exhibited relatively high variance among populations, suggesting potential local adaptation or environmental influence. These include leaf length (25.24%), total leaf length (19.80%), and total leaf width (17.75%). In contrast, certain traits showed little to no variation among populations (nut scar diameter, cupule width, cupule width/cupule height, and cupule height/cupule width ratios), indicating that these traits are likely highly conserved across populations. Several traits showed high variance among individual trees within populations (cupule height 57.69%, nut in cupule 56.48%, nut length 39.43%, nut diameter 38.89%), suggesting substantial tree-level phenotypic diversity. Finally, many traits exhibited high within-tree (residual) variability (number of lobes 70.51%, right-side base-to-widest-point distance 68.91%, incision width below maximum width on the left side 65.95%), possibly reflecting micro-environmental effects (Table 4).

The most stable traits within populations were related to leaves, specifically the right-side base-to-widest-point distance (WPD), and the incision width below maximum width on the left side (LIW). Nut traits showed greater variability, while the highest variability within populations was observed in cupule traits, such as nut in cupule (NIC) and cupule height (CH) (Table 4). The most stable traits among populations were associated with the cupule (cupule

Table 3. Summary statistics of the studied morphological traits of *Quercus petraea*

Trait	Minimum	Maximum	Mean	Standard Deviation	CV (%)
LL (mm)	61.00	260.00	90.74	14.09	15.53
PL (mm)	2.00	119.00	14.53	5.32	36.61
WPD (mm)	13.00	138.00	51.46	13.13	25.51
RW (mm)	12.00	59.00	28.36	5.23	18.44
LW (mm)	10.00	73.00	28.65	5.38	18.79
LIW (mm)	6.00	44.00	15.07	4.10	27.24
TLL (mm)	71.00	280.00	105.27	16.09	15.28
TLW (mm)	34.00	129.00	57.01	9.71	17.03
LW/LL	0.27	1.06	0.63	0.08	13.41
LL/LW	0.94	3.67	1.61	0.23	14.37
PL/LL	0.02	1.42	0.16	0.06	36.33
LN	1.00	8.00	6.08	1.19	19.63
NL (mm)	11.90	38.30	21.87	3.93	17.99
ND (mm)	8.30	22.80	13.26	1.89	14.24
NSD (mm)	3.70	15.00	6.90	1.23	17.90
ND/NL	0.37	1.02	0.62	0.10	15.71
NL/ND	0.98	2.74	1.66	0.27	16.33
CW (mm)	9.20	20.60	14.57	1.76	12.08
CH (mm)	2.50	18.60	7.94	1.80	22.62
NIC (mm)	1.50	10.80	6.14	1.59	25.94
CW/CH	0.76	5.12	1.92	0.48	25.04
CH/CW	0.20	1.31	0.55	0.12	21.99

Table 4. Proportion of variance components of traits based on data from seven natural populations of *Quercus petraea* in Bosnia and Herzegovina

Traits	Proportion of variance components			Population differentiation coefficient (%)	F value	
	Among populations	Among trees within populations	Within trees (residual)		Among populations	Among trees within populations
LL	25.24	37.64	37.12	40.14	190.31***	27.80***
PL	2.53	48.44	49.03	4.96	39.47***	27.12***
WPD	15.74	15.36	68.91	50.61	61.48***	6.89***
RW	12.99	25.48	61.53	33.76	62.40***	11.95***
LW	17.54	24.06	58.40	42.17	83.67***	11.89***
LIW	12.54	21.51	65.95	36.83	55.07***	9.62***
TLL	19.80	42.15	38.05	31.96	154.71***	30.29***
TLW	17.75	28.18	54.07	38.64	93.25***	14.78***
LW/LL	2.68	31.73	65.59	7.78	23.56***	13.79***
LL/LW	2.50	34.51	62.99	6.76	24.99***	15.48***
PL/LL	10.77	39.11	50.12	21.59	73.02***	21.63***
LN	4.11	25.38	70.51	13.93	24.46***	10.52***
NL	17.04	39.43	43.53	30.17	118.51***	24.95***
ND	9.64	38.89	51.47	19.86	65.75***	20.97***
NSD	0.00	44.41	55.59	0.00	21.38***	22.12***
ND/NL	4.33	47.15	48.52	8.41	48.06***	26.69***
NL/ND	3.52	52.15	44.33	6.32	51.11***	32.10***
CW	0.00	47.43	52.57	0.00	13.78***	24.86***
CH	0.94	57.69	41.37	1.61	43.36***	37.86***
NIC	10.08	56.48	33.43	15.15	117.79***	45.66***
CW/CH	0.00	56.72	43.28	0.00	35.17***	35.64***
CH/CW	0.46	55.37	44.18	0.82	36.65***	34.13***
Mean	8.64	39.51	51.84	18.70		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

width – CW), nut (nut scar diameter – NSD), and leaf shape (leaf width-to-length ratio – LW/LL). In contrast, the most variable traits among populations were related to leaves (leaf length – LL, total leaf length – TLL), nuts (nut length – NL), and cupules (nut in cupule – NIC) (Table 4).

Correlations among traits

Pearson correlation coefficients were calculated to assess relationships among phenotypic traits based on tree means, as shown in Figure 3. Significant correlations were found among traits within each group of traits – leaves, nuts, and cupules – but not between traits from different groups. The strongest correlations were observed among leaf traits, followed by cupule traits, while correlations among acorn traits were very low.

Principal components and cluster analysis of the traits

Principal component analysis (PCA) was performed to capture among-tree variation in the studied morphological traits, summarizing them into independent axes of variation (Table 5). The eigenvalues of the first six principal components were greater than 1, collectively accounting for 88.0% of the total variation. The primary axis of variation (PC1, 26.4%) was associated with leaf size, defined by length and width. The second component (PC2, 19.8%) contrasted cupule size with nut size traits, while leaf dimensions were intermediate. The third component (PC3, 13.0%) reflected leaf shape, distinguishing between large, narrow leaves and small, elongated ones.

The biplot constructed from the first two principal components is presented in Figure 4. Highly correlated leaf traits dominate the first component axis, while cupula traits contribute more strongly to the second component. In this two-dimensional space, the positions of populations indicate that the Bihać population, located at the lowest altitude, is characterized by the highest values of leaf traits. Longer and narrower nuts and cupules were attributable to the group of Kreševo, B. Krupa, and Ključ populations, whereas shorter and more expanded nut and cupule shapes characterized populations Tešanj, Bužim, and Sanski Most.

There is an overlap among all the studied populations in the two-dimensional space. The Bihać population is distinct from the others, while the Bužim Baštra population exhibits narrow variation in leaf dimension and a stronger tendency toward smaller nut and cupule traits (Fig. 5).

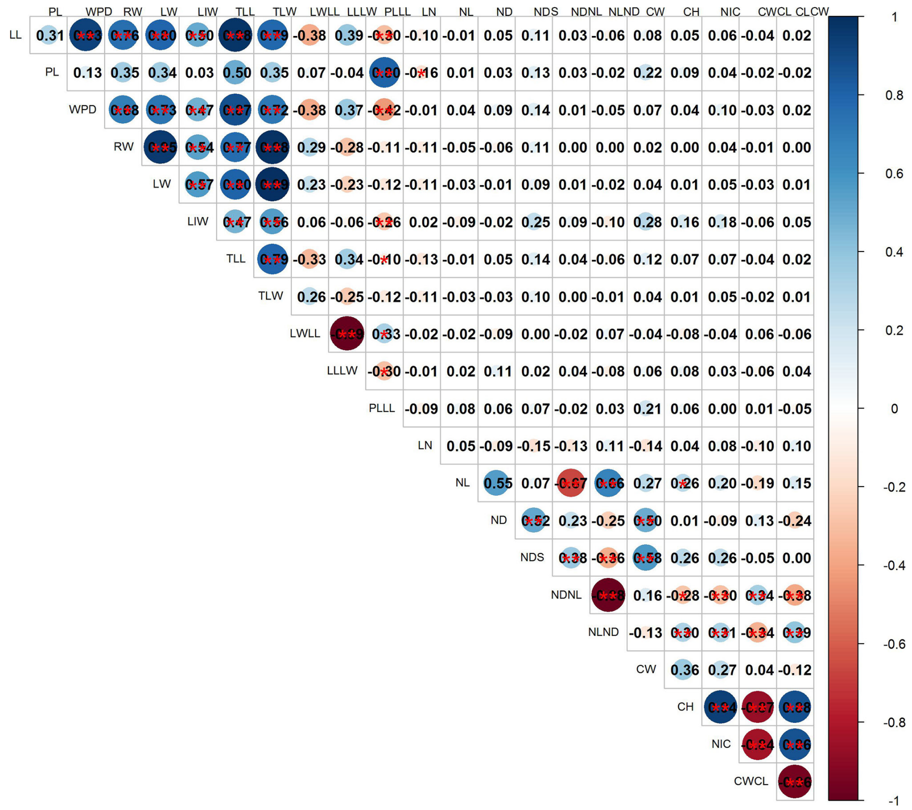

Fig. 3. Correlation analysis of phenotypic traits at the tree-level. Blue and red indicate positive and negative correlation, respectively, with darker colors representing stronger correlations (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

LL – leaf length; PL – petiole length; WPD – right-side base-to-widest-point distance; RW – right half-leaf maximum width; LW – left half-leaf maximum width; LIW – incision width below maximum width on the left side; TLL – total leaf length; TLW – total leaf width; LL/LW; LL/LW; LN – number of lobes; NL – nut length; ND – nut diameter; NDS – nut scar diameter; ND/NL; NL/ND; CW – cupule width; CH – cupule height; NIC – nut in cupule.

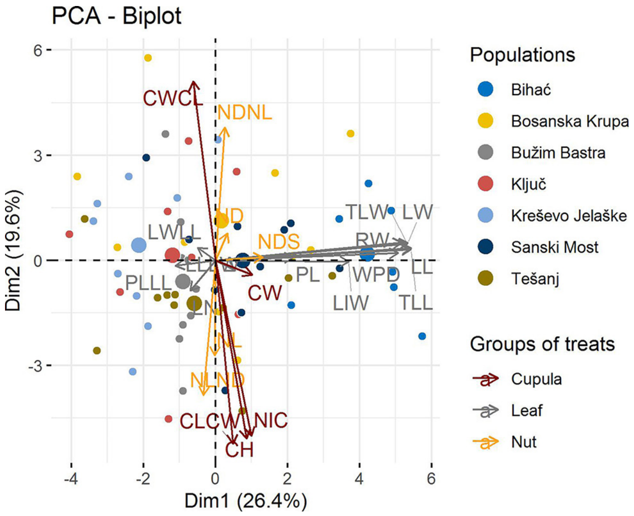

Fig. 4. Biplot of principal component analysis based on tree means of morphometric traits in *Quercus petraea* populations

LL – leaf length; PL – petiole length; WPD – right-side base-to-widest-point distance; RW – right half-leaf maximum width; LW – left half-leaf maximum width; LIW – incision width below maximum width on the left side; TLL – total leaf length; TLW – total leaf width; LL/LW; LL/LW; LN – number of lobes; NL – nut length; ND – nut diameter; NDS – nut scar diameter; ND/NL; NL/ND; CW – cupule width; CH – cupule height; NIC – nut in cupule.

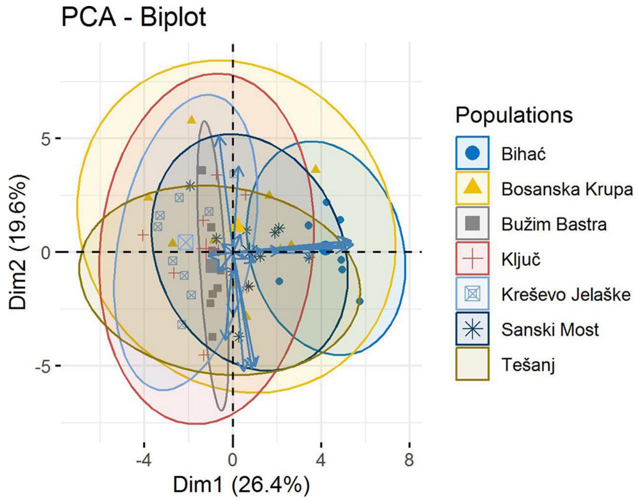

Fig. 5. Biplot of the principal component (PC) analysis based on tree means of morphometric traits in *Quercus petraea* populations

Table 5. Eigenvalues, contribution rates, and cumulative contributions of the first six principal components based on tree means for the studied traits

Traits	PC1	PC2	PC3	PC4	PC5	PC6
LL	0.389	0.019	0.147	0.105	0.066	0.085
PL	0.152	0.002	−0.170	−0.264	0.182	0.552
WPD	0.363	0.009	0.177	0.131	0.061	−0.052
RW	0.373	0.041	−0.223	0.027	−0.019	−0.060
LW	0.384	0.039	−0.185	0.027	−0.006	−0.057
LIW	0.268	−0.007	−0.006	−0.045	−0.151	−0.260
TLL	0.389	0.018	0.095	0.038	0.097	0.202
TLW	0.383	0.042	−0.206	0.026	−0.013	−0.061
LW/LL	−0.033	0.039	−0.535	−0.147	−0.109	−0.220
LL/LW	0.037	−0.035	0.534	0.122	0.118	0.234
PL/LL	−0.083	−0.010	−0.257	−0.338	0.170	0.470
LN	−0.044	−0.071	0.015	0.139	−0.031	−0.158
NL	−0.004	−0.223	0.010	−0.099	0.546	−0.262
ND	0.019	0.067	0.198	−0.372	0.283	−0.284
NSD	0.097	0.003	0.161	−0.454	−0.091	−0.184
ND/NL	0.020	0.314	0.154	−0.227	−0.391	0.054
NL/ND	−0.027	−0.319	−0.171	0.211	0.377	−0.059
CW	0.070	−0.036	0.138	−0.464	0.117	−0.128
CH	0.056	−0.424	0.073	−0.196	−0.166	0.018
NIC	0.065	−0.418	0.044	−0.145	−0.208	−0.010
CW/CH	−0.033	0.433	−0.007	0.008	0.219	−0.074
CH/CW	0.032	−0.435	0.001	0.025	−0.236	0.077
Eigen value	2.409	2.085	1.691	1.632	1.432	1.280
Contribution rate of variance	0.264	0.198	0.130	0.121	0.093	0.075
Cumulative proportion	0.264	0.461	0.591	0.712	0.806	0.880

Using the UPGMA method and based on standardized population means for the studied morphological traits, the seven populations were grouped into three clusters (Fig. 6). The first cluster comprised the Tešanj, Bužim Baštra, and Sanski Most populations; the second cluster included the Kreševo Jelaške, Bosanka Krupa, and Ključ populations; while the third cluster consisted solely of the Bihać population.

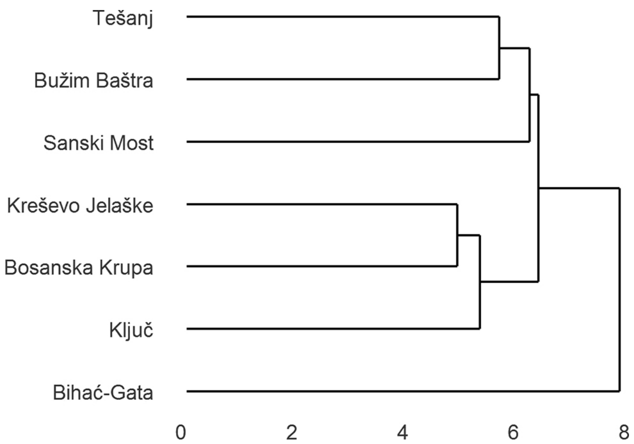

Fig. 6. Cluster relationship among the studied *Quercus petraea* populations based on the UPGMA method and analysed morphological traits. Euclidean distance was used to calculate phenotypic distances between populations

Euclidean distance was used as a part of the agglomerative hierarchical clustering performed with the „MorfoTools“, a set of R functions for morphometric analysis, following the manual by Koutecký (2015). The application of Manhattan and Minkowski distances, integrated in „MorphoTools2“ (Šlenker et al., 2022), produced consistent hierarchical clustering results, similar to those obtained using Euclidean distance.

Relations between morphology and climatic factors

Morphological variability of the analyzed traits at the population level was reduced to five principal components (dimensions), which together explained 97.6% of the total variation. The first component primarily represented leaf traits. Cupula traits were most strongly associated with the second component. The third and fourth components were mainly related to nut traits, while the fifth component was associated exclusively with cupule width (Fig. 7).

Figure 8 presents the correlations between principal components representing phenotypic traits of leaves and acorns (leaf size, cupule shape, nut size, nut shape, and cupule width) and bioclimatic variables ($p>0.01$). The first principal component,

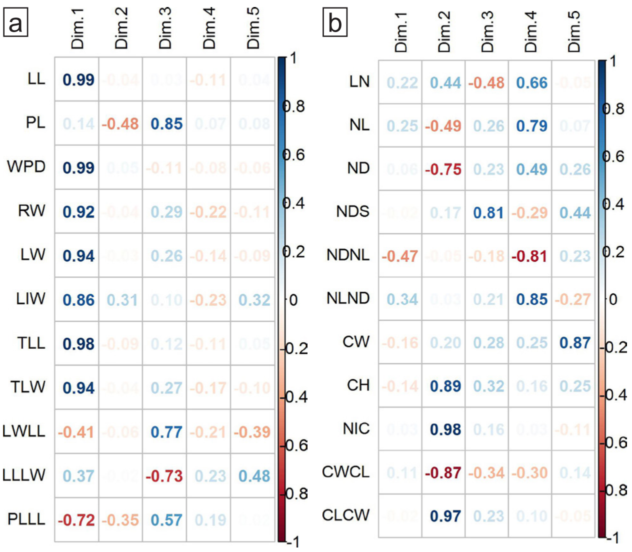

Fig. 7. Contributions of morphological variables to the principal components

(LL – leaf length; PL – petiole length; WPD – right-side base-to-widest-point distance; RW – right half-leaf maximum width; LW – left half-leaf maximum width; LIW – incision width below maximum width on the left side; TLL – total leaf length; TLW – total leaf width; LL/LW; LL/LW; LN – number of lobes; NL – nut length; ND – nut diameter; NDS – nut scar diameter; ND/NL; NL/ND; CW – cupule width; CH – cupule height; NIC – nut in cupule).

representing leaf size, showed statistically significant correlations with five temperature-related variables: BIO1 (Annual Mean Temperature), BIO5 (Max Temperature of Warmest Month), BIO9 (Mean Temperature of Driest Quarter), BIO10 (Mean Temperature of Warmest Quarter), and BIO11 (Mean Temperature of Coldest Quarter). Positive correlations indicate that increases in these temperature variables are

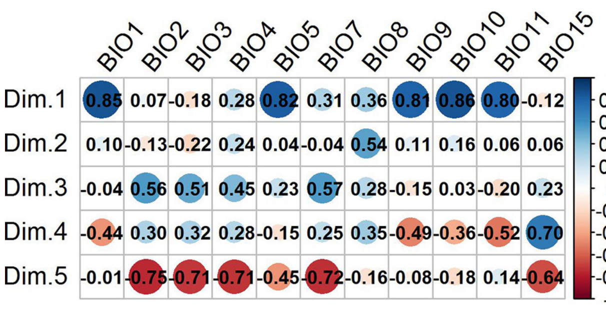

Fig. 8. Correlation analysis between climate variables and principal components. Blue and maroon indicate positive and negative correlation, respectively; darker shades represent stronger correlations (* p < 0.05; ** p < 0.01; *** p<0.001)

BIO1 – Annual Mean Temperature; BIO2 – Mean Diurnal Range; BIO3 – Iso-thermality; BIO4 – Temperature Seasonality; BIO5 – Max Temperature of Warmest Month; BIO7 – Temperature Annual Range; BIO8 – Mean Temperature of Wettest Quarter; BIO9 – Mean Temperature of Driest Quarter; BIO10 – Mean Temperature of Warmest Quarter; BIO11 – Mean Temperature of Coldest Quarter; BIO15 – Precipitation Seasonality.

associated with larger leaf sizes, suggesting that populations located in warmer climates in the western part of Bosnia and Herzegovina tend to have larger leaves.

Regression analysis was conducted to evaluate the relationships between the first principal component (representing leaf size) and the correlated climate variables. A linear stepwise regression identified the mean temperature of the warmest quarter as the best representative of the temperature-related variables. The regression model indicated that a one standard deviation increase in temperature corresponds to a 0.86 standard deviation increase in leaf size. Although the number of populations studied was limited, correlations between other principal components, representing nut and cupule dimensions and shapes, and climatic variables also suggested potential relationships.

Discussion

Phenotypic variation of traits

The coefficient of variation for measured leaf traits (excluding derived traits) in this study ranged from 15.53% for leaf length to 36.61% for leaf petiole length, indicating a relatively high degree of variability in leaf morphology within sessile oak populations in Bosnia and Herzegovina. In contrast, fruit traits showed lower variability, with coefficients ranging from 12.08% for cupule width to 25.94% for the nut in cupule trait. This reduced variation in fruit traits may be partly due to the sampling method, as only healthy, fully developed acorns, relatively uniform in size, were selected for analysis. The variation observed in cupule traits followed a similar pattern to that of the acorns, which is expected given their close morphological and developmental relationship. Phenotypic variation observed in leaf size and shape reflects the interaction of multiple genetic and environmental factors (Gonzalez et al., 2012). Previous studies have demonstrated that variations in these traits correspond to underlying genetic diversity and environmental heterogeneity (Wright, 2005; Niinemets & Sack, 2006; Reich et al., 2007; Niinemets, 2015). Furthermore, leaf size, morphology, structure, and orientation directly influence photosynthetic efficiency and significantly impact overall plant productivity (Marron & Ceulemans, 2006).

Phenotypic variation among and within populations

As hypothesized, this study revealed substantial phenotypic variation in leaf, nut, and cupule morphology both within and among populations. Variance components analysis identified three hierarchical levels of variability: among populations, among trees within populations, and within trees (residual variation). The largest share of variation occurred within trees (mean = 51.84%), followed by among trees within populations (mean = 39.51%), and the least among populations (mean = 8.64%), indicating a high degree of intra-individual plasticity and substantial tree-level diversity within populations. These results are consistent with earlier findings in pedunculate oak from Bosnia and Herzegovina (Ballian et al., 2010), where variation among trees within populations was consistently greater than variation among populations for all traits examined.

Some traits exhibited relatively high variance among populations (including leaf length with 25.24%, total leaf length with 19.80%, and total leaf width with 17,75% proportions of variance attributed to populations), suggesting potential local adaptation or environmental influence. In contrast, traits like nut scar diameter, cupule width, and cupule height to width ratios were highly conserved, with little variation among populations. Traits exhibiting the highest intrapopulation variation included cupule height (57.69%), nut in cupule (56.48%), nut length (39.43%), and nut diameter (38.89%). Many traits also displayed considerable residual (within-tree) variation, notably number of lobes (70.51%), right-side base-to-widest-point distance (68.91%), and left-size incision width (65.95%), possibly reflecting micro-environmental effects.

The most stable traits within populations were related to leaves, specifically the right-side base-to-widest-point distance (WPD), and the incision width below maximum width on the left side (LIW), indicating consistent leaf morphology among individuals within the same environment. Conversely, nut traits showed greater variability, while cupule traits, such as cupule height (CH) and nut in cupule (NIC), exhibited the highest variability within populations. Some authors have observed that fruit and seed traits exhibit more stable variation than leaf traits in certain species, such as *Eucommia ulmoides* (Wang et al., 2023) and *Malania oleifera* (Li et al., 2022), and have considered fruit and seed morphological traits more reliable to perform plus tree selection in breeding programs.

Across populations, the most stable traits were cupule (cupule width – CW), nut (nut scar diameter – NSD), and leaf shape (leaf width-to-length ratio – LW/LL). Conversely, the most variable traits among populations were (leaf length – LL, total leaf length – TLL), nuts (nut length – NL), and cupules (nut in cupule – NIC).

These phenotypic findings are consistent with previous genetic studies on sessile oak. Studies conducted in Bosnia and Herzegovina (Ballian et al., 2007; Ballian & Bogunić, 2012; Ballian, 2016) have documented both intra- and inter-population genetic variation. Comparable results from molecular marker analyses in Slovakia, Bulgaria, and Russia (Gömöry et al., 2001), Italy (Bruschi et al., 2003b), and Romania (Rebrean, 2023) likewise indicate that the majority of genetic variation is found within populations. This pattern supports the high level of intra-population morphological diversity observed in the present study.

Correlations among traits. The observed significant correlations within each trait group (leaves, nuts, and cupules) indicate these traits form distinct functional and developmental modules, evolving somewhat independently (Armbruster et al., 2014; Klingenberg, 2014). The strongest correlations among leaf traits likely reflect coordinated growth regulated by shared genetic and physiological controls, consistent with their role in photosynthesis and environmental adaptation (Nicotra et al., 2011; Wright et al., 2017). Similar patterns have been reported in other forest tree species, including *Castanea* sativa, where strong correlations were observed among leaf traits and within fruit and cupule structures, but rarely between them (Tuğ et al., 2022). A study of *Eucommia ulmoides* also found population-level correlations among leaf traits and fruit traits (Wang et al., 2023). In contrast, weaker correlations among acorn traits suggest more independent variation, possibly due to differing selective pressures on reproductive structures (Fenster et al., 2004). The lack of correlations between organ groups supports modularity, allowing sessile oak populations flexibility to adapt differentially across organ systems in response to diverse environmental and evolutionary pressures.

Principal components and cluster analysis of the traits

UPGMA clustering of populations, based on morphological traits, highlighted the Bihać population, located on the lowest altitude, as having the largest leaves. These differences align more with climatic factors than geography, with warmer, wetter areas supporting larger leaves. This supports leaf size as a climate-sensitive trait influenced by temperature and moisture, consistent with Wright et al. (2017), who showed larger leaves prevail in warm, moist environments due to thermal and hydraulic constraints. Our study supports these conclusions on a more localized scale, emphasizing the role of environmental filtering in shaping phenotypic diversity in forest tree species.

Similar relationships have been observed in other *Quercus petraea* populations (Arab et al., 2021; Niinemets, 2015), where leaf size increases with temperature and precipitation due to increased resource availability and reduced water stress. Interestingly, UPGMA clustering did not group populations according to their geographic proximity but instead formed clusters that likely reflect a combination of historical human disturbance and ecological site conditions. This suggests that local management practices, especially historical overexploitation (Begović, 1978), may have disrupted population structure and altered morphological norms.

Relations between morphology and climatic factors

Our results demonstrated strong internal correlations among leaf traits and consistent responses to climatic variables, particularly mean and maximum temperatures. Regression analyses confirmed that warmer climates (especially during the warmest quarter) are associated with larger leaf dimensions. These positive correlations indicate that increases in these temperature variables are associated with larger leaf sizes, suggesting that populations located in warmer climates in the western part of Bosnia and Herzegovina tend to have larger leaves. This pattern highlights a clear environmental signal in leaf morphology and underscores the ecological significance of temperature as a driver of phenotypic variation. These findings support our second hypothesis and align with prior evidence of high leaf plasticity in *Quercus petraea* in response to climate (Gonzalez et al., 2012; Wright et al., 2017; Arab et al., 2021).

In contrast, acorn and cupule traits showed lower variability and weaker correlations with climatic factors. This suggests that these traits may be more genetically canalized and subject to stronger stabilizing selection, a pattern also observed in other species (Wang et al., 2023; Li et al., 2022). These results are consistent with earlier findings that leaf shape and size are adaptive traits linked to growth and can serve as early indicators of biomass yield (Marron et al., 2007; Gebauer et al., 2016). Wright et al. (2017) demonstrated that leaf size varies predictably with climate, with larger leaves typically occurring in warm, moist environments, while smaller leaves are found in hotter, drier, or colder regions. Similarly, Ballian and Memišević Hodžić (2022) found a positive correlation between leaf size in natural populations of *Quercus robur* and growth traits (height and root collar diameter) in a provenance test derived from these populations. Ballian et al. (2018) reported population differentiation based on leaf traits that corresponded to climatic regions. This further supports the idea that leaf morphology reflects population adaptability to environmental conditions. In contrast, results from previous studies on acorn and cupule size have not established a link to climate change, indicating a notable gap in this area of morphological research.

Interpretation of our results must also take into account the complex taxonomy of *Q. petraea* in the Balkans. Although we relied on expert knowledge to identify and collect samples of *Quercus petraea*, other oak species capable of hybridizing with it are also present in the area. This taxonomic fluidity cautions against attributing all observed morphological variation solely to environmental adaptation. Future studies could benefit from incorporating molecular markers or geometric photometric approaches (e.g., Proietti et al., 2021) to clarify species boundaries and better resolve intra-aggregate structure.

The historical overharvesting of *Q. petraea* in Bosnia and Herzegovina (Begović, 1978) likely altered the structure of many populations. Selective removal of superior phenotypes and fragmentation of once-continuous forest stands may have reduced both genetic diversity and the expression of optimal traits. Anthropogenic reductions in population size can diminish genetic diversity and adaptive capacity (e.g., through selective logging, which effectively acts as a bottleneck) (Aravanopoulos, 2018; Allendorf et al., 2022; Konrad et al., 2025).

Conclusions

From a conservation standpoint, our results underscore the importance of preserving intra-population variability, the primary reservoir of adaptive potential in *Q. petraea.* While inter-population differences were modest, the phenotypic structuring observed along environmental gradients suggests the presence of some degree of local adaptation. These findings support the continued use of local seed sources for reforestation and the careful matching of planting material to site-specific environmental conditions, particularly in the context of an ongoing changing climate.

Further research integrating morphometric, genetic, and ecological data will be essential to resolve the taxonomic and adaptive landscape of *Q. petraea* in the Balkans. In the meantime, conservation strategies should prioritize preserving population integrity and local adaptation patterns, especially in ecologically marginal or historically disturbed sites.

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