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Correlation of pedunculate oak leaf traits *in situ* and *ex situ* in Bosnia and Herzegovina

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Abstract

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Pedunculate oak is an economically and ecologically very valuable species at the European level and for Bosnia and Hercegovina, and research into variation of this species is very important. In 2007, pedunculate oak leaf material was collected in 27 populations in Bosnia and Herzegovina along with seeds, which were used to establish a provenance trial. In the trial, leaves were collected in 2021, and 14 morphological traits were measured in both types of material. Analysis of variance showed generally non-significant differences between generations, but significant variation among populations and population-by-generation interactions. However, the correlations between generations were non-significant for most traits, and neither were the correlations with climatic parameters. The results indicate both genetic and environmental effects on leaf morphology. The utility of leaf morphology for gene conservation is shortly discussed.

Keywords

leaf morphological traits, natural populations, provenance test, *Quercus robur*

Introduction

Pedunculate oak (*Quercus robur* L.) is a species with a large distribution, reaching northwards to southern Norway and Sweden, and southwards to the northern part of the Iberian Peninsula, South Italy, the Balkan Peninsula and Turkey. Compared to *Quercus petraea* it reaches more northerly ranges on the Norwegian coast and in northern Scotland; in Mediterranean areas it is also present in Portugal, Greece and South Turkey, and eastwards into continental central Russia, up to the Urals. The southerly range limits are difficult to define, as these oaks can mix, compete and naturally hybridise with other Mediterranean oaks, such as *Quercus pubescens* and *Quercus frainetto*. Therefore, it shows great variability as it grows in extremely contrasting ecological conditions (Eaton et al., 2016). Wood quality makes it one of the most prized deciduous species in the northern temperate climate zone (Eaton et al., 2016). Pedunculate oak is also valued as a species, which can show relatively good drought resistance (Matthias et al., 2011), and thus a species that is gaining in importance in the afforestation of areas affected by climate change.

There are relatively few pedunculate oak forests

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in Bosnia and Herzegovina, about 30,000 ha (Klepac, 1988). These woods are the remnants of once large forest areas under the pedunculate oak that have historically disappeared or have been degraded by large-scale fellings (Ballian and Memišević Hodžić, 2016). According to estimates (Memišević Hodžić and Ballian, 2018), about 5% of Bosnia and Herzegovina are plains suitable for the growth of pedunculate oak, while areas where pedunculate or mixed pedunculate oak-hornbeam forests (*Carpino betuli – Quercetum roboris*) are potential vegetation amount to 598,276 ha, i.e., 11.7% of the area of Bosnia and Herzegovina according to ecological-vegetation regionalization (Stefanović et al., 1983). Bosnian oak forests are proximate to the glacial refugia of oaks (Petit et al., 2002); as such, they represent valuable genetic resources deserving special attention.

Table 1. List of investigated provenances

No	Populations/ Provenances	Latitude	Longitude	Altitude (m asl)
1	Bijeljina	44º43’50”	19º13’30”	93
2	Bosanska Dubica	45º06’24”	16º40’32”	145
3	Bosanska Gradiška	45º07’04”	17º19’03”	91
4	Bosanski Brod	45º05’30”	18º03’00”	84
5	Bosansko Grahovo	44º01’05”	16º38’24”	703
6	Bugojno	44º06’00”	17º26’31”	537
7	Drvar	44º23’39”	16º21’54”	462
8	Hrgovi Srebrenik	44º49’06”	18º34’11”	133
9	Jelah	44º39’09”	17º56’46”	181
10	Kaćuni	44º03’59”	17º56’13”	443
11	Kiseljak	43º56’30”	18º04’56”	477
12	Ključ	44º30’56”	16º48’42”	260
13	Knežina	44º01’40”	18º44’53”	759
14	Kotor Varoš	44º39’07”	17º21’35”	252
15	Lukavica	43º49’26”	18º21’58”	552
16	Miljevina Foča	43º31’06”	18º38’56”	627
17	Mrkonjić Grad	44º27’04”	16º58’42”	753
18	Mutnica Cazin	44º58’55”	15º50’54”	270
19	Nević Polje	44º11’46”	17º42’11”	476
20	Novi Šeher	44º30’09”	18º02’02”	230
21	Olovo	44º07’44”	18º36’11”	542
22	Sokolac	43º55’17”	18º 48’53”	866
23	Stojčevac Ilidža	43º48’40”	18º17’25”	506
24	Vinac	44º15’48”	17º17’08”	408
25	Visoko Muhašinovići	44º00’38”	18º08’45”	413
26	Žepče	44º25’35”	18º03’10”	224
27	Živinice	44º27’58”	18º41’09”	216
Trial site	Nursery Žepče	44º25’00”	18º00’00”	232

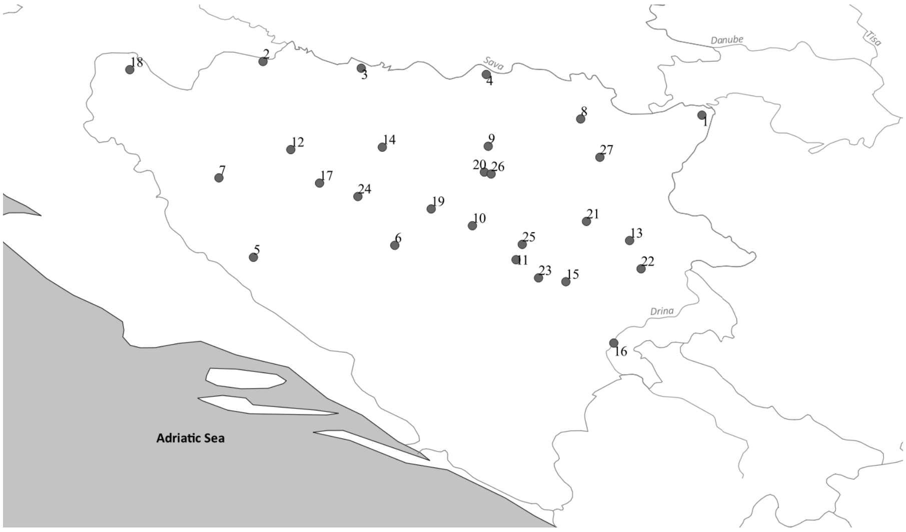

Fig. 1. Investigated populations/provenances in Bosnia and Herzegovina.

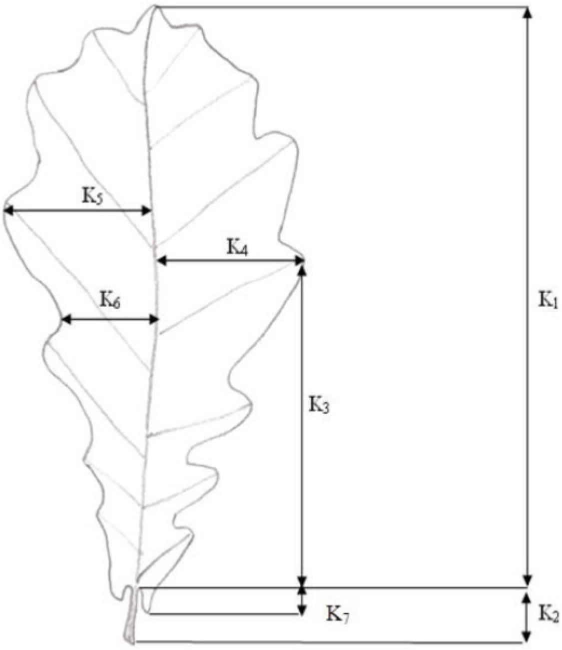

Fig. 2. Measured leaf traits.

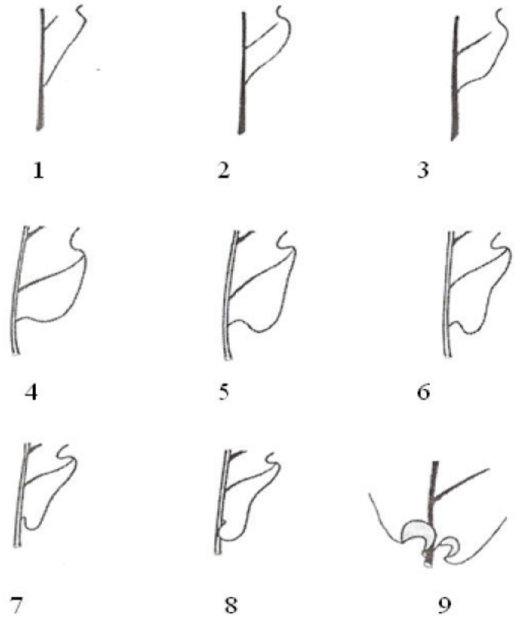

Fig. 3. Leaf base shape (Kremer et al., 2002).

Considering this fact, restoration of pedunculate oak forests is planned, while successful reintroduction requires phenotypic and molecular characterization of existing genetic resources.

Earlier research on the morphological properties of pedunculate oak leaves showed differences in leaf morphology in natural populations in Bosnia and Herzegovina (Ballian et al., 2015; 2017). Molecular analysis using nuclear microsatellites confirmed a large morphological variability of pedunculate oak in Bosnia and Herzegovina (Ballian et al., 2010). Popović et al. (2023) found a high intra-population diversity (98.53%) and a small but statistically significant interpopulation differentiation analyzing 10 nuclear and 9 chloroplast SSRs in a field trial.

A provenance trial was established to investigate the variability of pedunculate oak in Bosnia and Herzegovina. The results of research on provenance trial confirmed a strong interprovenance differentiation, both at the molecular level (Memišević Hodžić and Ballian, 2019; Memišević Hodžić et al., 2021) and the phenotypic level (Memišević Hodžić and Ballian, 2020). Vegetative phenology also exhibited variation among the studied provenances and years (Memišević Hodžić and Ballian, 2018), which indicates both hereditary effects on leafing properties and effects of seasonal variation in climate.

Heritability of leaf morphological traits is generally moderate to strong in trees (Guet et al., 2015; Migicovsky et al., 2018; Ren et al., 2020). This also applies to oaks (Santaigne et al., 2004; Klápště et al., 2021), and makes leaf morphology, along with molecular markers, a useful tool for the characterization of genetic resources of oaks. However, a prerequisite for practical applicability is the existence of strong inter-population variation at morphological traits (if possible, geographically structured; geographical trends or patterns are an advantage in this respect) and their ontogenetical stability.

This study addresses both topics – it aims to assess the level of interpopulation variation in leaf morphological traits of pedunculate oak in natural populations (*in situ*) and a provenance test raised from these populations (*ex-situ*), and to quantify the population-level correlations in these traits between generations.

Materials and methods

In the first part of this study we measured morphological traits of pedunculate oak leaves from 27 populations in Bosnia and Herzegovina. The populations are distributed across the whole pedunculate oak range in Bosnia and Herzegovina, and cover different ecological vegetation areas (Stefanović et al., 1983; Table 1, Fig. 1).

Leaf material was collected in natural populations also in 2007 from solitary trees or trees on forest edges, as previous research has shown that such material is most suitable for morphometric analysis and represents well the studied populations (Franjić, 1994; Franjić et al., 2000). Medium-sized leaves from a short fertile shoot were collected. Ten leaves per tree were measured from 10 trees per population. The following traits were measured (Figs 2 and 3): K1 – leaf blade length, K2 – leaf petiole length, K3 – the distance of the widest part of the blade from the blade base (on the right side), K4 – maximum width of the right half-blade, K5 – maximum width of the left half-blade, K6 – incision of the leaf from the central nerve, K7 – incision of the leaf base. Calculated traits: K8 – total leaf blade width (K4 + K5), K9 – total leaf length (K1 + K2), K10 – the ratio of leaf width and length (K8 / K1), K11 – average lobe length (K1 / K12). Counted traits: K12 – number of lobes on the right side. Assessed traits: K13 – hairiness (1 – no hairiness, 2 – leaf axillary hairiness, 3 – whole leaf hairiness), K14 – leaf base shape (1–9, Fig. 3).

Basic climatic data (Table S1) were taken from the nearest meteorological stations (source: Stefanović et al. 1983).

Pedunculate oak seed was collected in the same 27 natural populations were the leaves were collected. The seed was sown in a forest nursery at 2007. Provenance experiment was established in 2009 with one-year-old seedlings. In 2021 leaf material was collected in the provenance test from 13-years-old plants. The leaves from side shoots in the insolated parts of the crowns were taken. An identical set of traits was measured on leaves from the provenance test as from natural population.

Data were processed in the statistical program SAS (SAS, 2004). Descriptive statistics were calculated using the procedure MEANS. Analysis of variance (ANOVA; population and generation being the main effects, both considered fixed, the random effect of tree was nested within population) and a subsequent nested ANOVA by populations were performed using the GLM procedure. Provenance-level correlations between leaf morphological properties in natural populations and their offspring in the provenance experiment, as well as correlations between morphological traits and climatic data were calculated using the CORR procedure based on population means. Principal component analysis (PCA) based on leaf traits was performed using the procedure PRINCOMP; trait K13 was omitted from PCA. Geographical distribution of the first two principal components in adults as well as in the offspring were displayed using the program QGIS 3.14 (https://qgis.org/en/site/).

Results

Basic statistics of the assessed traits are shown in Table 2. In natural populations (adults), there was no variation in leaf hairiness (K13), trees were consistently hairless, although individuals with axillary or whole-leaf hairiness were found among the offspring. Therefore, this trait was excluded from further comparisons.

As the interaction was mostly significant, separate ANOVAs were done by populations. The results (significances of *F*-tests) are shown in Table 4. The between-generation differences are inconsistent among populations; they are highly significant for 11 out of 13 traits in Bijeljina, Jelah, Kaćuni, Knežina or Srebrenik, but only for 5 traits in Ključ.

As the parent-progeny relationships between the adults in natural populations and offspring in the provenance test were unknown, only population-level correlations between generations were calculated based on population averages of traits (Table 5). Generally, positive correlations between populations and offspring were quite rare, they were observed only for leaf blade length (K1), total leaf length (K9) and average lobe length (K11).

Correlations between morphological traits and climatic parameters of the sites of origin were only exceptionally significant (Table S2) and none of them remained

Table 2. Descriptive statistics for leaf traits in natural populations and in the provenance test

Variable	N	Natural populations (adults)		Provenance experiment (offspring)	
		Mean	Std.dev	Mean	Std.dev
K1 (mm)	27	80.72	13.07	79.39	3.89
K2 (mm)	27	4.01	0.66	6.53	0.46
K3 (mm)	27	48.32	8.25	45.30	2.67
K4 (mm)	27	24.15	3.99	23.79	1.18
K5 (mm)	27	23.90	4.22	23.95	1.21
K6 (◦)	27	9.70	1.65	12.48	0.94
K7 (◦)	27	1.24	0.42	3.51	0.55
K8 (mm)	27	84.72	13.32	47.74	2.37
K9 (mm)	27	48.05	8.18	85.92	3.91
K10	27	0.60	0.01	0.61	0.04
K11 (mm)	27	17.27	2.36	14.91	0.94
K12	27	4.84	0.30	5.48	0.28
K13	27	1.00	0.00	1.12	0.07
K14	27	7.15	0.91	5.51	0.35

Table 3. ANOVA analysis for leaf traits

Mean	Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
K1	pop	25	431,728.74	17,269.15	31.85	<0.0001
	gen	1	3,735.01	3,735.01	0.35	0.5611
	pop*gen	25	269,043.35	10,761.73	19.85	<0.0001
	tree(pop*gen)	468	253,757.30	542.22	12.32	<0.0001
	error	10,278	452,323.51	44.01		

Table 3 – Continued

Mean	Source	DF	Sum of Squares	MeanSquare	F Value	Pr > F
K2	pop	25	1,453.12	58.12	3.90	<0.0001
	gen	1	12,672.03	12,672.03	295.26	<0.0001
	pop*gen	25	1,072.97	42.92	2.88	<0.0001
	tree(pop*gen)	468	6,972.38	14.90	14.41	<0.0001
	error	10,278	10,626.15	1.03		
K3	pop	25	162,885.94	6,515.44	18.33	<0.0001
	gen	1	16,846.84	16,846.84	3.52	0.0725
	pop*gen	25	119,737.71	4,789.51	13.47	<0.0001
	tree(pop*gen)	468	166,382.86	355.52	4.55	<0.0001
	error	10,278	802,286.47	78.06		
K4	pop	25	36,055.14	1,442.21	18.95	<0.0001
	gen	1	303.46	303.46	0.26	0.6156
	pop*gen	25	29,348.96	1,173.96	15.42	<0.0001
	tree(pop*gen)	468	35,618.62	76.11	7.71	<0.0001
	error	10,278	101,443.92	9.87		
K5	pop	25	41,136.09	1,645.44	20.41	<0.0001
	gen	1	0.99	0.99	0.00	0.9782
	pop*gen	25	32,600.25	1,304.01	16.17	<0.0001
	tree(pop*gen)	468	37,734.49	80.63	8.28	<0.0001
	error	10,278	100,043.61	9.73		
K6	pop	25	8,004.92	320.20	6.11	<0.0001
	gen	1	15,801.24	15,801.24	71.27	<0.0001
	pop*gen	25	5,542.99	221.72	4.23	<0.0001
	tree(pop*gen)	468	24543.16	52.44	6.67	<0.0001
	error	10,278	80,832.06	7.86		
K7	pop	25	699.79	27.99	4.93	<0.0001
	gen	1	10,129.92	10,129.92	241.21	<0.0001
	pop*gen	25	1,049.92	42.00	7.40	<0.0001
	tree(pop*gen)	468	2,656.01	5.68	7.78	<0.0001
	error	10,278	7,501.98	0.73		
K8	pop	25	375,863.16	15,034.53	32.15	<0.0001
	gen	1	2,728,839.29	2,728,839.29	212.78	<0.0001
	pop*gen	25	320,617.13	12,824.69	27.43	<0.0001
	tree(pop*gen)	468	218,826.88	467.58	18.92	<0.0001
	error	10,278	254,029.18	24.72		
K9	pop	25	193,519.80	7,740.79	20.20	<0.0001
	gen	1	2,845,904.79	2,845,904.79	632.25	<0.0001
	pop*gen	25	112,530.57	4,501.22	11.75	<0.0001
	tree(pop*gen)	468	179,346.46	383.22	8.06	<0.0001
	error	10,278	488,643.72	47.54		
K10	pop	25	4.38	0.18	0.79	0.7608
	gen	1	0.28	0.28	1.88	0.1823
	pop*gen	25	3.67	0.15	0.66	0.8961
	tree(pop*gen)	468	104.32	0.22	0.78	0.9999
	error	10,278	2,952.16	0.29		
K11	pop	25	16,573.15	662.93	9.40	<0.0001
	gen	1	11,348.40	11,348.40	34.53	<0.0001
	pop*gen	25	8,217.18	328.69	4.66	<0.0001
	tree(pop*gen)	468	32,993.73	70.50	9.83	<0.0001
	error	10,278	73676.81	7.17		
K12	pop	25	365.02	14.60	2.57	<0.0001
	gen	1	831.31	831.31	73.98	<0.0001
	pop*gen	25	280.91	11.24	1.98	0.0036
	tree(pop*gen)	468	2,660.12	5.68	7.98	<0.0001
	error	10,278	7,317.37	0.71		
K14	pop	25	1,884.81	75.39	9.25	<0.0001
	gen	1	5,499.67	5,499.67	78.35	<0.0001
	pop*gen	25	1,754.80	70.19	8.61	<0.0001
	tree(pop*gen)	468	3,813.83	8.15	9.07	<0.0001
	error	10,278	9,234.28	0.90		

Table 4. Summary of F-tests of differences between adults and offspring by populations (nested ANOVA)

Trait	Source of variation	Bijeljina	Bos. Brod	Bos. Dubica	Bos. Gradiska	Bos. Grahovo	Bugojno	Cazin Stojcevac	Drvar Mutnica	Ilidza Stojcevac
K1	gen	<0.0001	<.0001	0.3107	0.4927	0.3395	0.0052	0.7106	0.0378	0.0005
K2	gen	0.0008	0.0007	0.0016	0.0003	<0.0001	<0.0001	0.0009	0.0502	0.0091
K3	gen	0.0004	<.0001	0.1801	0.0048	0.0186	0.5692	0.1586	0.0045	0.0419
K4	gen	0.0015	<.0001	0.0438	0.0671	0.0076	0.0334	0.2199	0.0593	0.9348
K5	gen	0.0008	<.0001	0.1478	0.3742	0.0101	0.0063	0.1205	0.0320	0.5241
K6	gen	0.0133	0.6296	0.0047	0.5381	0.0004	0.0003	0.0018	<0.0001	0.0187
K7	gen	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0001	<0.0001	<0.0001	<0.0001
K8	gen	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
K9	gen	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0002
K10	gen	0.8265	0.0848	0.1818	0.1969	0.0628	0.8313	0.4571	0.5545	0.5234
K11	gen	0.0064	0.0003	0.0027	0.0014	0.2528	0.9107	0.0291	0.5412	0.0708
K12	gen	0.5603	0.9172	0.0069	0.0228	0.1971	0.0897	0.0199	0.9902	0.0271
K14	gen	<0.0001	1.0000	0.0083	0.0063	0.0006	<0.0001	0.0531	0.0057	<0.0001

Table 4. Continued

Trait	Source of variation	Jelah	Kacuni	Kiseljak	Kljuc	Knezina	Kotor Varos	Lukavica	Miljevina	Nevic Polje
K1	gen	0.0022	<0.0001	<0.0001	0.7461	<0.0001	0.9009	0.4099	0.5954	<0.0001
K2	gen	0.0002	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<.0001	<0.0001
K3	gen	0.0005	0.0001	0.0002	0.7977	0.0245	0.0006	0.2588	0.0242	0.0953
K4	gen	0.0274	<0.0001	0.0038	0.2331	0.0068	0.0129	0.7415	0.7285	0.0022
K5	gen	0.0266	<0.0001	0.0113	0.1815	<0.0001	0.0264	0.2777	0.4697	0.0016
K6	gen	0.0002	<0.0001	0.0002	<0.0001	0.0005	0.1423	0.0004	0.0012	<0.0001
K7	gen	<0.0001	<0.0001	0.2184	<0.0001	<0.0001	<0.0001	<0.0001	<.0001	<0.0001
K8	gen	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<.0001	<0.0001
K9	gen	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<.0001	<0.0001
K10	gen	0.6036	0.4338	0.5458	0.2446	0.7373	0.6590	0.7751	0.6917	0.8807
K11	gen	0.0074	0.7637	0.2997	0.2087	0.3636	0.0027	0.0010	0.0250	0.4116
K12	gen	0.3610	0.0001	0.0031	0.1949	0.0190	0.0025	<0.0001	0.0198	0.0038
K14	gen	<0.0001	<0.0001	0.0006	0.3057	<0.0001	<0.0001	0.0585	0.0277	<0.0001

Table 4. Continued

Trait	Source of variation	Olovo	Seher	Sokolac	Srebrenik	Vinac	Visoko	Zepce	Zivinice
K1	gen	0.0385	0.0028	0.0180	0.0005	0.0018	0.2533	<0.0001	<0.0001
K2	gen	<0.0001	0.0013	0.0015	<0.0001	0.0008	<0.0001	<0.0001	0.0545
K3	gen	0.6686	0.0070	0.6508	0.0002	0.2519	0.0010	<0.0001	<0.0001
K4	gen	0.0753	0.1194	0.0001	0.0348	0.0024	0.1122	<0.0001	<0.0001
K5	gen	0.0107	0.3235	0.0002	0.0122	0.0003	0.2137	<0.0001	<0.0001
K6	gen	0.0004	0.0141	0.0001	0.8675	0.0005	0.0013	0.7052	0.2247
K7	gen	<0.0001	<0.0001	<0.0001	0.0006	<0.0001	<0.0001	<0.0001	<0.0001
K8	gen	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
K9	gen	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
K10	gen	0.7369	0.2113	0.1113	0.3051	0.2764	0.7843	0.3854	0.1274
K11	gen	0.0184	<0.0001	0.0765	<0.0001	0.5532	0.0979	<0.0001	0.0028
K12	gen	0.0059	0.0005	0.0023	0.0057	0.0082	0.0134	0.5842	0.8898
K14	gen	0.0331	<0.0001	0.2639	<0.0001	0.0022	0.0060	<0.0001	0.2239

Table 5. Pearson’s coefficient of correlation between populations and their offspring

Trait	K1	K2	K3	K4	K5	K6	K7	K8
r	0.46784	0.15885	0.30793	0.20294	0.22401	0.21524	– 0.16620	0.23831
P	0.0139	0.4287	0.1181	0.3100	0.2613	0.2810	0.4074	0.2313
Trait	K9	K10	K11	K12	K14			
r	0.38231	0.11805	0.49521	0.14162	0.08002			
P	0.0491	0.5576	0.0086	0.4811	0.6915			

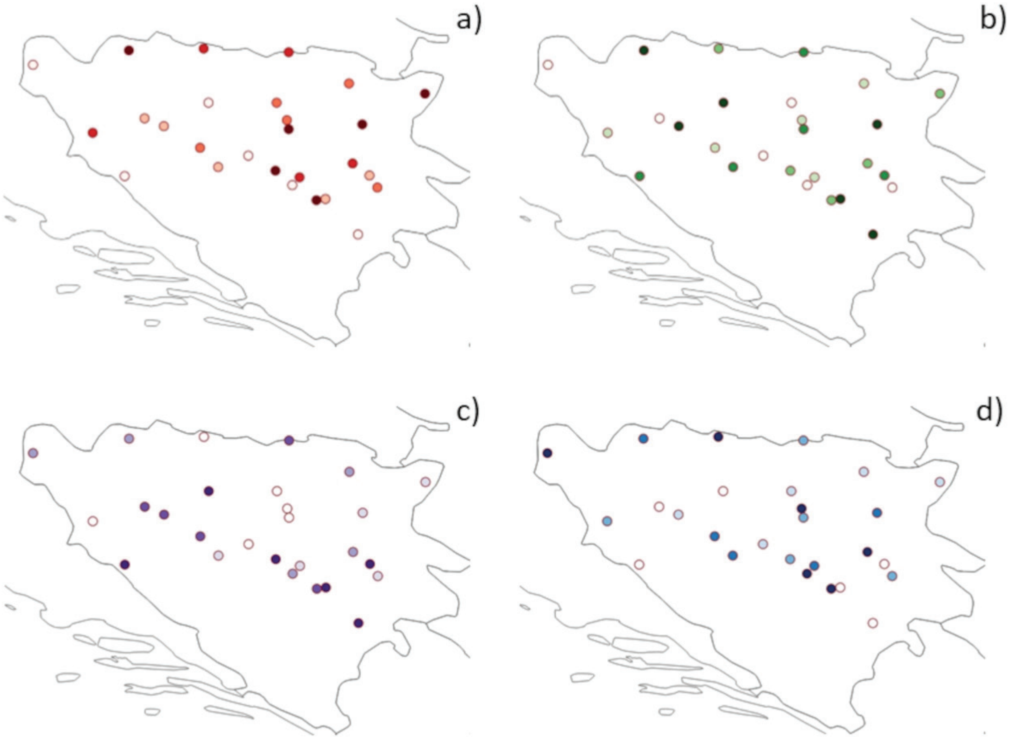

Fig. 4. Geographical distribution of principal coordinate scores: a) PC1 in adults, b) PC2 in adults, c) PC1 in the offspring, d) PC2 in the offspring.

significant after Bonferroni correction for multiple testing. The same applies to geographical trends – no correlations with geographical coordinates were observed.

First two principal components contributed almost equally to the total variance (35.02% and 33.07% for PC1 and PC2, respectively), while the contribution of the other PCs was considerably smaller. Population means of principal component score do not exhibit any geographical patterns or trends (Fig. 4).

Discussion

In the systematics of the genus *Quercus*, leaf morphology is important for the discrimination of species and subspecific taxa (Kremer et al., 2002; Ponton et al., 2004; Curtu et al., 2011; Apostol et al., 2017). This implies that leaf traits, besides the effects of ecological factors, are under strong genetic control. To what extent this applies also to the within-taxon level is unclear. Phenotypic variation is a common feature of any species, both at the individual and population levels. Distinguishing genetic and environmental effects underlying this variation is not necessarily easy, especially when organisms and their populations are studied *in situ*.

The outcomes of our study in terms of signals for hereditary control of leaf morphology are not unambiguous. Admittedly, the material used in this study is not ideal for addressing the issue of hereditary vs. environmental control of phenotypic traits. The *ex situ* plantation was not established as a combined provenance-progeny test, i.e., the identity of maternal trees of individuals planted in the provenance trial is unknown. Consequently, the heritability of leaf traits based on parent-offspring correlations could not be assessed, and any assumption about the genetic component of leaf morphology variation can only rely on indirect evidence. On one hand, for all traits except the leaf width-to-length ratio, significant interpopulation variation across generations was found; such variation is observed frequently (Coart et al., 2002; Apostol et al., 2017) but not always (Enescu et al., 2010). Abdeljalil and Beghami (2022) found significant variations in morphological traits of leaves among two *Quercus* species, but not between the species, which indicates that the morphological evolution of both species could be attributed to climatic change and stand conditions. Natural populations occur *in situ*, the variation among them may be caused not only by genetic effects but can be attributed to environmental variation as well. However, in the *ex-situ* plantation (provenance test), all provenances grow in identical meso-scale environment (while the design of the experiment is expected to compensate for microsite variation). Common patterns of leaf morphology across generations and sites are thus an indication of hereditary control. There is also a huge intrapopulation variation, while the distributions of traits are generally continuous and nearly normal, but this is an expected outcome when the control of traits is polygenic, which is in agreement with the findings of Scotti-Santaigne et al. (2004) or Gailing et al. (2008). On the other hand, population-by-generation interaction was also generally highly significant, which means that the variation patterns differed between generations. Moreover, population-level correlations between generations were generally weak. Such inter-generation shifts in leaf morphology are not exceptional (Boratynski et al., 2008); in our case, they are probably related to environmental differences between the sites of origin and the sites of plantation and demonstrate phenotypic plasticity, which is a typical feature of long-lived organisms such as forest trees (Aubin-Horth and Renn, 2009). This is not a reliable argument against genetic control of leaf traits, as the extent of sharing genes between the adult and juvenile individuals is unknown, but the gene pools of the parental and the offspring generation under random mating are expected to be identical. Under a strong genetic control of the intrapopulation variation in leaf morphology, significant correlations would be expected to appear also at the population level.

Significant variation among populations at least in the offspring generation, where the provenances are planted in a homogeneous environment, indicates the existence of the genetic component of the variation in leaf morphology, which may rely both on neutral and adaptive processes. Our results give little evidence for adaptation. Neither clear geographical patterns in leaf morphology nor correlations with climatic parameters were observed. More plausibly, the background is neutral. Historical bottlenecks are improbable, Bosnia and Hercegovina is situated in the proximity of the Balkan glacial refugia (Petit et al., 2002), so the territory was colonized early in the Holocene, and oak forests expanded on suitable sites. However, during the Middle Ages, oak forests suffered from overexploitation (FAO, 2015; Ballian and Memišević Hodžić, 2016); consequently, the distribution range became shrunken and fragmented, the size of many populations decreased and gene flow among them was disturbed. Recent bottlenecks cannot thus be excluded. Another factor contributing to the genetic component of variation is interspecific hybridization. White oak species (*Quercus* subgenus *Quercus*) are known to share substantial part of their nuclear as well as organellar genomes (Kremer and Petit, 1993; Gömöry and Schmidtová, 2007). Hybridization was even suggested to be a mechanism of colonization in white oaks (Petit et al., 2003). The range of *Q. robur* in Bosnia almost completely overlaps with the range of at least two other white oak species: *Q. petraea* and *Q. pubescens*. Different levels of introgression may also have contributed to the observed morphological differentiation among pedunculate oak populations, although this contribution is unlikely to be significant; as shown by Gugerli et al. (2007), despite extensive sharing of the nuclear genome, survival of interspecific hybrids in mixed stands is limited.

Whatever is the background mechanism behind the significant interpopulation variation demonstrated in this study, leaf morphology as a type of traits, which can easily be scored on a large scale without a need for sophisticated devices or expensive chemicals, may be a good tool for practical purposes. For instance, Ballian and Memišević Hodžić (2022) found positive provenance-level correlations between most leaf morphological properties in natural populations and plant height and root neck diameter in the offspring planted in the provenance test. This suggests that leaf morphology may guide the selection of appropriate genetic resources for practical use.

Conclusions

Variation among populations was highly significant for most traits except for the ratio of leaf width and length.

Consistent differences between natural stands and *ex situ* plantations were observed for leaf petiole length, incision of the leaf from the central nerve, incision of the leaf base, total leaf blade width, total leaf length, average lobe length, number of lobes on the right side, and leaf base shape.

Population-by-generation interaction was significant for all traits except the ratio of leaf width and length, meaning that the difference between natural stands and *ex situ* plantations was population-specific.

The between-generation differences are inconsistent among populations; they are highly significant for 11 out of 13 traits in Bijeljina, Jelah, Kaćuni, Knežina or Srebrenik, but only for five traits in Ključ.

As the parent-progeny relationships between the adults in natural populations and offspring in the provenance test were unknown, only population-level correlations between generations were calculated based on population averages of traits. Generally, positive correlations between populations and offspring were quite rare, they were observed only for leaf blade length, total leaf length, and average lobe length.

Correlations between morphological traits and climatic and geographic parameters of the sites were not significant.

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Supplementary material

Table S1. Climatic data for the meteorological station near populations and provenance test (highlighted in grey)

Population	The nearest meteo-station	Average air temperature (ºC)		Average relative air humidity (%)		Average sum of precipitation mm		Vegetation period (days)
		Yearly	IV–IX	Yearly	IV–IX	Yearly	IV–IX	
Bosanska Gradiška	B.Gradiška	10.6	17.2	–	–	831	457	185
Bosanski Brod	Doboj	10.5	16.9	80	76	995	534	200
Jelah	Tešanj	9.6	15.9	–	–	1,069	579	180
Bosanska Dubica	B.Dubica	10.2	16.7	80	75	946	508	195
Mrkonjić Grad	B.Luka	10.5	16.9	78	74	1,057	559	197
Kotor Varoš	Kotor Varoš	10.3	16.4	81	78	1,081	613	196
Bijeljina	Bijeljina	10.9	17.9	81	87	751	413	202
Miljevina Foča	Foča	9.9	15.8	83	79	885	385	191
Cazin Mutnica	Bihać	10.7	16.8	76	72	1,347	586	204
Ključ	Ključ	9.7	17.2	–	–	1,284	711	181
Bugojno Kopčić	Bugojno	8.8	14.8	78	74	826	383	174
Vinac	Bugojno	8.8	14.8	78	74	826	383	174
Kiseljak	Fojnica	8.2	14.1	–	–	1,234	522	165
Kaćuni	Fojnica	8.2	14.1	–	–	1,234	522	165
Žepče	Zenica	10.3	16.6	76	72	804	416	197
Visoko	Sarajevo	9.7	15.5	72	67	946	450	186
Nević polje	Travnik	8.8	15.0	77	73	881	441	179
Ilidža Stojčevac	Sarajevo	9.7	15.5	72	67	946	450	186
Lukavica	Sarajevo	9.7	15.5	72	67	946	450	186
Srebrenik Hrgovi	Brčko	11.2	17.9	79	74	781	429	211
Živinice	Tuzla	10.2	16.3	76	73	921	522	197
Sokolac	Sokolac	6.5	12.8	81	78	804	430	147
Olovo	Pržići	7.1	13.4	–	–	1,183	567	162
Knežina	Sokolac	6.5	12.8	81	78	804	430	147
Drvar	Drvar	9.4	15.5	77	73	1,135	529	184
Bosansko Grahovo	B.Grahovo	8.2	13.9	68	64	1,356	558	166
Novi Šeher	Zenica	10.3	16.6	76	72	804	416	197

Table S2. Correlations between climatic parameters / geographical coordinates of the sites of origin and morphological traits in natural populations and provenances of pedunculate oak

Trait		TEMPy	TEMP$_{49}$	AIR_Hy	AIR_H$_{49}$	PRECy	PREC$_{49}$	VEG_PER	LAT	LONG	ALT
Natural populations (adults)											
K1	*r*	0.13453	0.12577	0.0302	0.10051	-0.1957	-0.11146	0.17249	0.15124	0.26467	-0.28883
	P	0.5035	0.5319	0.8966	0.6647	0.3279	0.5799	0.3896	0.4514	0.1822	0.144
K2	*r*	0.25665	0.26681	-0.01885	0.09072	-0.15049	0.09295	0.25465	0.43668	0.13358	-0.4194
	P	0.1963	0.1785	0.9353	0.6957	0.4537	0.6447	0.1999	0.0228	0.5065	0.0294
K3	*r*	0.13851	0.12401	-0.03667	0.01823	-0.13277	-0.06112	0.16871	0.16585	0.18691	-0.27815
	P	0.4908	0.5377	0.8746	0.9375	0.5091	0.762	0.4002	0.4084	0.3505	0.1601
K4	*r*	0.18263	0.17452	0.07524	0.12088	-0.25693	-0.16606	0.21151	0.18262	0.23765	-0.29836
	P	0.3619	0.384	0.7458	0.6017	0.1958	0.4078	0.2896	0.3619	0.2326	0.1306
K5	*r*	0.18458	0.17448	0.0018	0.07909	-0.22497	-0.15	0.21234	0.14798	0.24875	-0.29261
	P	0.3567	0.3841	0.9938	0.7333	0.2592	0.4552	0.2876	0.4614	0.2109	0.1386
K6	*r*	0.34545	0.31121	-0.14542	-0.05597	-0.19445	-0.08643	0.38755	0.26862	0.20254	-0.4557
	P	0.0776	0.1141	0.5294	0.8096	0.3311	0.6682	0.0458	0.1755	0.311	0.0169
K7	*r*	0.00146	0.03512	-0.21174	-0.10844	0.24174	0.1368	0.00651	-0.21178	0.10176	-0.02713
	P	0.9942	0.8619	0.3568	0.6399	0.2244	0.4963	0.9743	0.2889	0.6135	0.8932
K8	*r*	0.14476	0.13668	0.02888	0.10306	-0.19949	-0.10471	0.18191	0.17013	0.26631	-0.30425
	P	0.4713	0.4966	0.9011	0.6567	0.3185	0.6032	0.3638	0.3962	0.1794	0.1228
K9	*r*	0.18417	0.17501	0.03747	0.0996	-0.24121	-0.15827	0.21256	0.1653	0.24406	-0.29627
	P	0.3578	0.3826	0.8719	0.6675	0.2255	0.4304	0.2871	0.41	0.2199	0.1335
K10	*r*	0.3325	0.31435	0.00423	-0.02168	-0.31779	-0.33555	0.30271	0.08798	-0.04032	-0.06833
	P	0.0902	0.1103	0.9855	0.9257	0.1062	0.0871	0.1248	0.6626	0.8417	0.7349
K11	*r*	0.03056	0.02732	0.0095	0.10117	-0.12189	-0.05239	0.03963	0.02464	0.34611	-0.22317
	P	0.8797	0.8924	0.9674	0.6626	0.5447	0.7952	0.8444	0.9029	0.077	0.2632
K12	*r*	0.29369	0.26711	-0.00442	-0.00527	-0.23583	-0.19701	0.35882	0.34864	-0.07745	-0.25983
	P	0.1371	0.178	0.9848	0.9819	0.2363	0.3246	0.0661	0.0747	0.701	0.1906
K14	*r*	-0.04355	-0.02518	-0.26303	-0.16015	0.27504	0.09978	-0.05352	-0.23777	0.00091	0.00196
	P	0.8292	0.9008	0.2493	0.488	0.165	0.6205	0.7909	0.2324	0.9964	0.9923
Provenances (offspring)											
K1	*r*	-0.05189	-0.09906	0.24043	0.17362	0.02299	0.00522	-0.01613	0.02818	0.13557	-0.18992
	P	0.7971	0.623	0.2938	0.4517	0.9094	0.9794	0.9363	0.889	0.5002	0.3427
K2	R	-0.12171	-0.16122	0.16202	0.18765	-0.11075	-0.18045	-0.03161	-0.04236	0.15871	0.12742
	P	0.5453	0.4218	0.4829	0.4153	0.5824	0.3677	0.8756	0.8338	0.4291	0.5265
K3	*r*	0.11222	0.12464	0.31006	0.15997	-0.04712	0.04277	0.13557	0.10513	0.13598	-0.30783
	P	0.5773	0.5356	0.1714	0.4885	0.8155	0.8323	0.5002	0.6018	0.4989	0.1183
K4	*r*	-0.38988	-0.45258	0.26805	0.17607	0.05204	-0.24334	-0.29483	-0.29984	0.12024	0.27631
	P	0.0444	0.0178	0.2401	0.4452	0.7966	0.2213	0.1355	0.1286	0.5502	0.163
K5	*r*	-0.34891	-0.41703	0.17057	0.10989	0.04802	-0.25577	-0.27147	-0.2767	0.07198	0.23556
	P	0.0745	0.0305	0.4598	0.6354	0.812	0.1979	0.1708	0.1624	0.7212	0.2369
K6	*r*	-0.21279	-0.17783	0.46731	0.45814	-0.03612	-0.16608	-0.13692	0.0274	0.15542	-0.00947
	P	0.2866	0.3749	0.0327	0.0367	0.858	0.4077	0.4959	0.8921	0.4389	0.9626
K7	*r*	-0.20299	-0.26572	-0.19333	-0.20219	-0.10885	-0.3289	-0.12196	-0.23976	-0.01482	0.36628
	P	0.3099	0.1804	0.4011	0.3794	0.5889	0.0939	0.5445	0.2284	0.9415	0.0602
K8	*r*	-0.37196	-0.43674	0.21677	0.14166	0.05354	-0.24642	-0.28617	-0.29014	0.09372	0.25729
	P	0.0561	0.0227	0.3453	0.5402	0.7908	0.2153	0.1479	0.1421	0.6419	0.1951
K9	*r*	-0.06593	-0.11751	0.25849	0.19415	0.00982	-0.01607	-0.01975	0.02303	0.15357	-0.17394
	P	0.7439	0.5594	0.2579	0.3991	0.9612	0.9366	0.9221	0.9092	0.4444	0.3856
K10	*r*	-0.33547	-0.38163	-0.27933	-0.25697	0.22064	-0.1169	-0.32787	-0.41988	0.04698	0.38328
	P	0.0871	0.0495	0.2201	0.2608	0.2688	0.5615	0.095	0.0292	0.816	0.0484
K11	*r*	-0.17387	-0.13674	0.2844	0.39059	0.07865	0.13513	-0.12212	0.06202	0.30332	-0.18666
	P	0.3858	0.4964	0.2115	0.08	0.6966	0.5016	0.544	0.7586	0.1241	0.3512
K12	*r*	0.16299	0.08667	-0.04699	-0.19433	-0.11125	-0.18295	0.1222	-0.01448	-0.20873	0.01219
	P	0.4166	0.6673	0.8397	0.3986	0.5807	0.361	0.5437	0.9429	0.2961	0.9519
K14	*r*	-0.2404	-0.21227	0.11507	0.2008	-0.27893	-0.41879	-0.15484	-0.25535	0.28168	0.3216
	P	0.2271	0.2878	0.6194	0.3828	0.1589	0.0297	0.4406	0.1986	0.1546	0.1019

TEMPy – mean annual temperature; TEMP$_{49}$ – mean temperature during the vegetation period (April to September); AIR_Hy – mean annual air humidity; AIR_H$_{49}$ – mean air humidity during the vegetation period; PRECy – yearly precipitation total; PREC$_{49}$ – precipitation total during the vegetation period; VEG_PER – vegetation period length; LAT – latitude; LONG – longitude; ALT – altitude.