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Morphometric analysis of leaf indumentum distinguishes greyish oak (*Quercus pedunculiflora* K. Koch) and pedunculate oak (*Quercus robur* L.) across their Central-Eastern European range

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Abstract

White oaks are keystone species in European lowland forests. The micro-morphology of pedunculate oak (*Quercus robur* L.) and greyish oak (*Quercus pedunculiflora* K. Koch), two closely related taxa sometimes treated as subspecies, was compared in the present paper. Greyish oak – distributed in the Balkans and Asia Minor – is proposed as a climate-resilient substitute for *Q. robur* L. under intensifying droughts. For our study, we collected leaf samples from populations in Hungary, Romania and Bulgaria, and compared them using indumentum characteristics, focusing on trichome types as potential diagnostic markers for forestry practice. Morphological observations of trichome rays collected at standardised sampling plots were compared using either classical statistics (countable measurements) or morphological classification (trichome types). Three trichome types were present on greyish oak: glandular and simple-uniseriate, stellate, and fasciculate trichomes, whereas pedunculate oak predominantly displayed simple-uniseriate trichomes, except for one intermediate individual. On average, the simple-uniseriate trichome rays on the leaf epidermis of *Q. pedunculiflora* K. Koch measured 79.81 µm in length, while the same in *Q. robur* L. were found to be 67.41 µm; a difference that was statistically significant. Fasciculate trichomes (mean length 274.99 µm) were diagnostic for *Q. pedunculiflora* K. Koch, despite occasional stellate trichomes in transitional forms (mean length 149.55 µm). These results confirm robust micromorphological differentiation between the taxa, validating trichome traits as reliable identification tool. The denser indumentum of greyish oak may reflect drought adaptation, highlighting its potential for assisted gene-flow in climate-smart forestry. The clear morphological difference in leaf indumentum can help practicing foresters to distinguish between the two oaks.

Key words: drought-tolerance; micromorphology; trichome; tree species replacement; species discrimination

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1. Introduction

Our climate is changing rapidly resulting in – amongst others – extreme weather conditions that are predicted to become more and frequent (IPCC 2021). This change is affecting the Central-Eastern European region, where the climate is predicted to become especially dry and hot during the summers (Bartholy et al. 2014). A particular way for forest management to effectively combat the negative effects of climate change is the use of more drought-tolerant tree species as a replacement of the current flora (Keenan 2015). In this respect, the pedunculate oak (*Quercus robur* L.) is significant but vulnerable element of the central-eastern European lowland forest flora (Doniță et al. 2003) to climate change, which otherwise produces irreplaceable timber for wood furniture industry (Molnár et al. 2016). The lowland pedunculate oak stands are located at the xeric limit and consequently exhibit heightened vulnerability to prolonged periods of drought (Bartha et al. 2018; Mátyás et al. 2018).

A close relative of the pedunculate oak (*Quercus robur* L.) is the greyish oak (*Quercus pedunculiflora* K. Koch), which is sometimes referred to as the subspecies of the former (i.e. *Q. robur* L. subsp. *pedunculiflora* [K. Koch]

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Menitsky) and reported to be more drought tolerant (Mátyás 1967; Curtu et al. 2011; Apostol et al. 2017). This tolerance can be a result of adaptation to drier climatic conditions at the more south-easterly distribution (Asia Minor and the Balkans) of this taxon (Schwarz 1937; Georgescu & Morariu 1948; Jalas & Suominen 1976). Greyish oak can be a potential replacement for pedunculate oak in the Carpathian Basin, on a more north-westerly area, where currently only pedunculate oak is dominating in native lowland forests (Doniță et al. 2003). Although the presence of greyish oak has been hypothesised from Hungary, especially on the eastern part of the country (Gencsi & Vancsura 1992), this has never been formally tested.

Quercus pedunculiflora was originally described by Koch (1849) from the Caucasus Mts. (Dagestan) and distinguished from pedunculate oak by its bluish-grey abaxial leaf indumentum. However, Menitsky (1984), who also noted the differences on the abaxial surface, later considered these differences to be insignificant characters and thus classified greyish oak as a subspecies of the pedunculate oak. He considered the indumentum of the abaxial leaf surface to be an adaptive difference between the two taxa, potentially highly variable due to eco-geographical factors. Trichome characteristics and leaf shape were reported to be tightly linked to climatic conditions in oaks (Martín-Sánchez et al. 2024a). The hairiness of vegetative and generative organs in greyish oak is well documented, and it has been suggested to be linked to tolerance of summer drought (Georgescu & Morariu 1948; Enescu 2017; Apostol 2019). In an initial study, Curtu et al. (2011) found the abaxial laminar pubescence to be a highly discriminatory character between the taxa, but they did not characterise this morphological difference in detail.

More recently, Apostol et al. (2017) revealed distinct morphological variations in Romania that allowed for clear taxonomic differentiation between the two taxa: abaxial pubescence and leaf color were identified as key differentiators. The study provided a detailed assessment of leaf pubescence, indicating that *Q. robur* L. has almost no hair, with only some unicellular trichomes present on the abaxial surface. In contrast, *Q. pedunculiflora* K. Koch exhibited densely pubescent unicellular and fasciculate trichomes with the abaxial leaf color showing bluish-green to bluish hues, which may correlate with the presence of trichomes. According to Krasilnikov (1957), the bluish-greyish colour of the abaxial side is not of indumentum origin, but the result of precipitation of a wax layer on the epidermis. A smooth wax layer was indeed observed on greyish oak specimens studied in the Zagros Mts., Iran (Mehrina et al. 2013), and also in our previous study (Hegedüs et al. 2023). However, this crystalline layer was identified in both greyish and pedunculate oak. The type of wax layer is influenced by temperature, and due to its plasticity, its use, as a micromorphological identifying character, is only possible with reservations. A comparison of abaxial leaf characters shows that the presence or absence of the indumentum is a more stable determinant.

Therefore, this study aims to (1) quantify and statistically compare the detailed morphological characteristics of abaxial leaf indumentum in *Quercus robur* L. and *Q. pedunculiflora* K. Koch populations from Bulgaria, Hungary, and Romania, (2) elucidate the specific morphological features that differentiate these taxa, particularly in the context of potential *Q. pedunculiflora* K. Koch presence in Hungary, and (3) evaluate the efficacy of abaxial leaf surface characteristics as reliable diagnostic tools for species identification in forestry practices.

2. Materials and methods

2.1. Plant material

Samples for morphometric analyses were collected during the summer of 2023 in three countries: Bulgaria, Hungary and Romania (Fig. 1). In Bulgaria, we focused on the northern part of the country, where mostly *Quercus robur* L. is reported (Yurukov & Zhelev 2001; Aleksandrov & Tonchev 2024), and the selection of individuals was recommended by Dr Rossen Tzonev (University of Pleven, Bulgaria) on the field. In Romania, the dissertation of Apostol (2019) was utilised as a foundation for the collection of samples from greyish oak in the southern part of the country, to locate forests with greyish oak stands on the Romanian Plain (Southern Romania). In Hungary, the research was centred on two forests: the "Peszér" Forest at Kunpeszér and the "Nagyerdő" in Debrecen, both renowned as old oak forests on the Hungarian Great Plain. In the former forest, we were guided by Dr Sándor Bordács (Institute of Agronomy, Hungarian University of Agriculture and Life Sciences, Hungary), who recommended us individuals that were judged by him as greyish oaks, pedunculate oaks, and intermediates. In Debrecen, old individuals were selected from the forest following the advice of Dr László Papp (Botanical Gardens, University of Debrecen, Hungary). At each sampling site, old (i.e. >120 years) trees that were likely to be native were selected.

In addition, a focus was placed on a selection of specimens from both the interior and the forest edges, with tree heights ranging from 25 to 35 m. Using a height pruner, we collected light leaves of similar size and shape from the lower-central parts of the crown of all individuals that were immediately pressed in an herbarium press. Additional, healthy leaves from the same trees were put into silica-gel for future DNA isolation. All specimens have been identified "*a priori*" as belonging to *Quercus robur* L. or *Quercus pedunculiflora* K. Koch or "intermediate" based on the expert opinion of the above local colleagues. This classification was

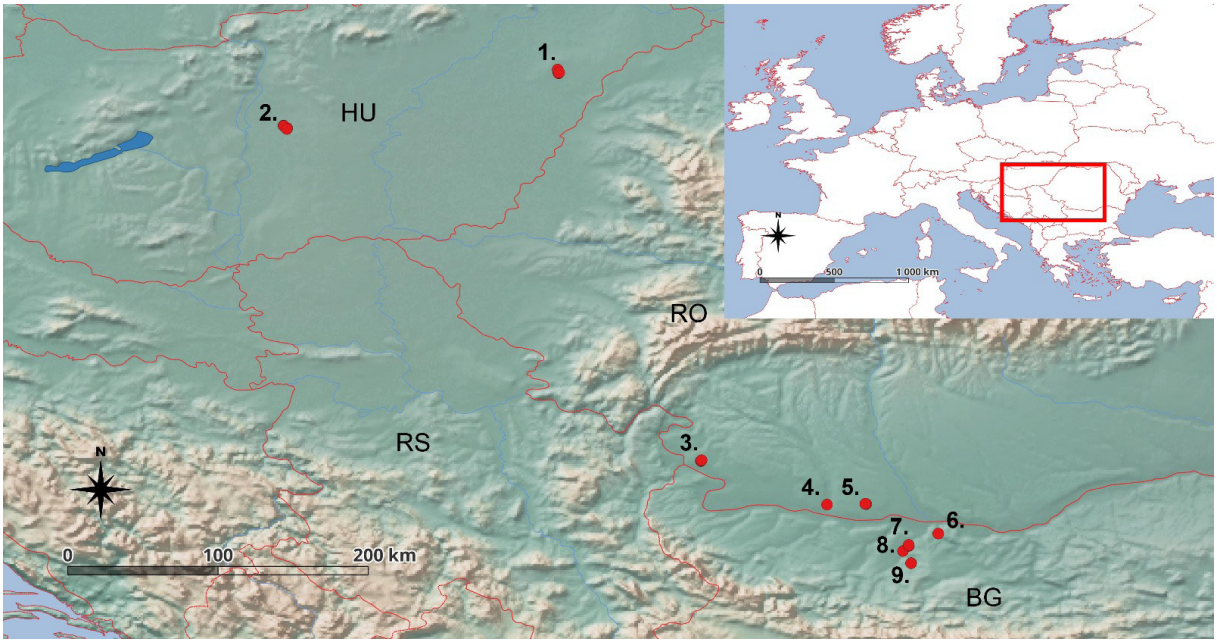


Fig. 1. Map of sampling sites of pedunculate and greyish oaks in Central-Eastern Europe (1. Debrecen Nagyerdő; 2. Peszéri-erdő; 3. Poiana Gruii; 4. Piscul Sadoveii; 5. Câmpu Părului; 6. Muselievo; 7. Komarevo; 8. Bivolare and Riben; 9. Pleven). The insert shows the study area's position in Europe. Country codes are given according to ISO-2 standards.

later re-evaluated based on the trichomes (presence of three types of trichomes or only one type, see Results) for an "*a posteriori*" identification, which was used for statistical calculations based on countable characters to group specimens (Table 1).

2.2. Morphological data collection

After drying and pressing, we took high-resolution images using an Olympus SZX7 stereo microscope at 5× magnification with a Canon EOS2000D camera at approximately the same five positions on the abaxial side of the leaves. The locations for taking the images were: (a) next to the midrib on the right side on the first lobule, (b) on the third lobule on the right side, (c) at the leaf apex, (d) on the third lobule on the left side, and (e) on the lowest lobule on the left side (Fig. 2).

Trichome morphology was studied, and measurements were made in the software ImageJ v.1.54g (Schneider et al. 2012). At each sampling locations on the leaf, the length of trichome rays was measured in an area of 3 mm^2 and the measurements from the five points were averaged. The same 3 mm^2 sampling plot was used to categorise trichomes into morphological classes (Fig. 3). All statistical calculations and data visualisations were performed in PAST v.4.06b (Hammer et al. 2001).

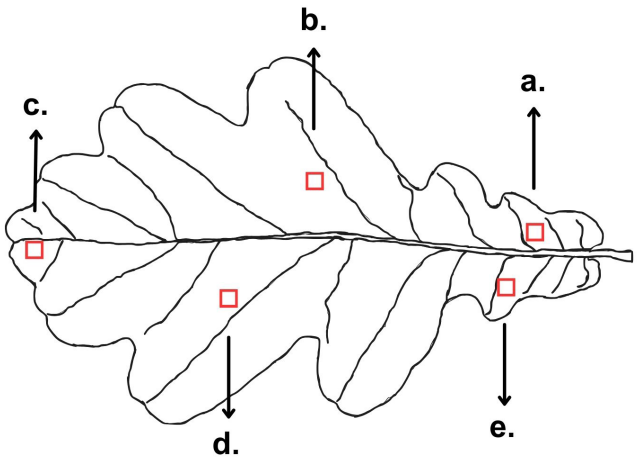


Fig. 2. Schematic leaf showing the approximate positions of micro-morphological images.

Table 1. List of samples used in this study with locality information, sample code, *a priori* and *a posteriori* taxonomic identification and trichome characteristics including qualitative (+ present; – absent) and basic quantitative (trichome density) measures. Boldface typing highlights differences between *a priori* and *a posteriori* classification.

A priori species classification	Locality (sampling code on Fig. 1)	Identification code	Glandular, simple-uniseriate trichome	Stellate trichome	Fasciculate trichome	Number of trichomes (No/mm^2)	*A posteriori* species classification
Quercus robur	BG: Bivolare: Vit river plain (8.)	K4438	+	–	–	43	*Quercus robur*
Quercus robur	BG: Bivolare: Vit river plain (8.)	K4439	+	–	–	37	*Quercus robur*
Quercus robur	BG: Riben (8.)	K4440	+	+	+	164	***Quercus pedunculiflora***
Quercus robur	BG: Riben (8.)	K4441	+	+	+	175	***Quercus pedunculiflora***
Quercus robur	BG: Komarevo to Podem roadside (7.)	K4442	+	+	–	105	*Quercus* sp. (*"transitional"*)
Quercus robur	BG: Komarevo to Podem roadside (7.)	K4443	+	+	+	199	***Quercus pedunculiflora***
Quercus robur	BG: Muselievo roadside (6.)	K4444	+	+	+	79	***Quercus pedunculiflora***
Quercus robur	BG: Muselievo roadside (6.)	K4445	+	–	–	35	*Quercus robur*
Quercus robur	BG: Pleven: public park (9.)	K4446	+	–	–	10	*Quercus robur*
Quercus robur	BG: Pleven: public park (9.)	K4447	+	–	–	60	*Quercus robur*
Quercus robur	BG: Pleven: public park (9.)	K4448	+	–	–	12	*Quercus robur*
Quercus robur	RO: Piscul Sadovei (4.)	K4449	+	–	–	40	*Quercus robur*
Quercus robur	RO: Campu Parului (5.)	K4450	+	+	+	95	***Quercus pedunculiflora***
Quercus robur	RO: Campu Parului (5.)	K4451	+	+	–	124	***Quercus*** sp. (***"transitional"***)
Quercus pedunculiflora	RO: Poiana Gruii (3.)	K4452	+	+	+	104	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Poiana Gruii (3.)	K4453	+	+	–	103	***Quercus*** sp. (***"transitional"***)
Quercus pedunculiflora	RO: Poiana Gruii (3.)	K4454	+	+	+	133	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Poiana Gruii (3.)	K4455	+	+	+	110	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Poiana Gruii (3.)	K4456	+	+	+	162	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Poiana Gruii (3.)	K4457	+	+	+	198	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Poiana Gruii (3.)	K4458	+	+	+	210	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Poiana Gruii (3.)	K4459	+	+	+	168	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Poiana Gruii (3.)	K4460	+	+	+	349	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Campu Parului (5.)	K4461	+	+	+	277	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Campu Parului (5.)	K4462	+	+	+	213	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Campu Parului (5.)	K4464	+	+	+	128	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Campu Parului (5.)	K4465	+	+	+	172	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Campu Parului (5.)	K4466	+	+	+	163	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Campu Parului (5.)	K4468	+	+	+	97	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Campu Parului (5.)	K4469	+	+	+	242	*Quercus pedunculiflora*
Quercus pedunculiflora	RO: Campu Parului (5.)	K4470	+	+	+	331	*Quercus pedunculiflora*
Quercus robur	HU: Kunpeszér (2.)	K4495	+	–	–	49	*Quercus robur*
Quercus robur	HU: Kunpeszér (2.)	K4496	+	–	–	3	*Quercus robur*
Quercus robur	HU: Kunpeszér (2.)	K4497	+	–	–	61	*Quercus robur*
Quercus robur	HU: Kunpeszér (2.)	K4498	+	–	–	31	*Quercus robur*
Quercus robur	HU: Kunpeszér (2.)	K4499	+	–	–	30	*Quercus robur*
Quercus pedunculiflora	HU: Kunpeszér (2.)	K4500	+	–	–	31	***Quercus robur***
Quercus pedunculiflora	HU: Kunpeszér (2.)	K4501	+	–	–	12	***Quercus robur***
Quercus pedunculiflora	HU: Kunpeszér (2.)	K4502	+	–	–	68	***Quercus robur***
Quercus pedunculiflora	HU: Kunpeszér (2.)	K4503	+	–	–	23	***Quercus robur***
Quercus sp. (*"transitional"*)	HU: Kunpeszér (2.)	K4504	+	–	–	50	***Quercus robur***
Quercus sp. (*"transitional"*)	HU: Kunpeszér (2.)	K4505	+	–	–	14	***Quercus robur***
Quercus robur	HU: Debrecen: Botanical Garden (native tree) (1.)	K4506	+	–	–	10	*Quercus robur*
Quercus robur	HU: Debrecen: Botanical Garden (native tree) (1.)	K4507	+	–	–	75	*Quercus robur*
Quercus robur	HU: Debrecen: Botanical Garden (native tree) (1.)	K4508	+	–	–	33	*Quercus robur*
Quercus robur	HU: Debrecen: Botanical Garden (native tree) (1.)	K4509	+	+	–	213	***Quercus*** sp. (***"transitional"***)
Quercus robur	HU: Debrecen: Botanical Garden (native tree) (1.)	K4510	+	–	–	15	*Quercus robur*
Quercus robur	HU: Debrecen: Nagyerdő: Medve-sarok (1.)	K4511	+	–	–	10	*Quercus robur*
Quercus robur	HU: Debrecen: Auguszta (1.)	K4512	+	–	–	49	*Quercus robur*

3. Results

Three trichome types were observed on the abaxial leaf surface of the studied specimens: (1) glandular and simple-uniseriate, (2) stellate, and (3) fasciculate trichomes (Table 1). Pedunculate oak possessed only glandular and simple-uniseriate trichomes, whereas greyish oak displayed all above trichome types (Fig. 3). The glandular and simple-uniseriate trichomes of *Quercus robur* L. were 67.41 µm, while the same trichome on *Q. pedunculiflora* K. Koch was 79.81 µm with a certain overlap in these values between the two species (Fig. 4). However, the differ-

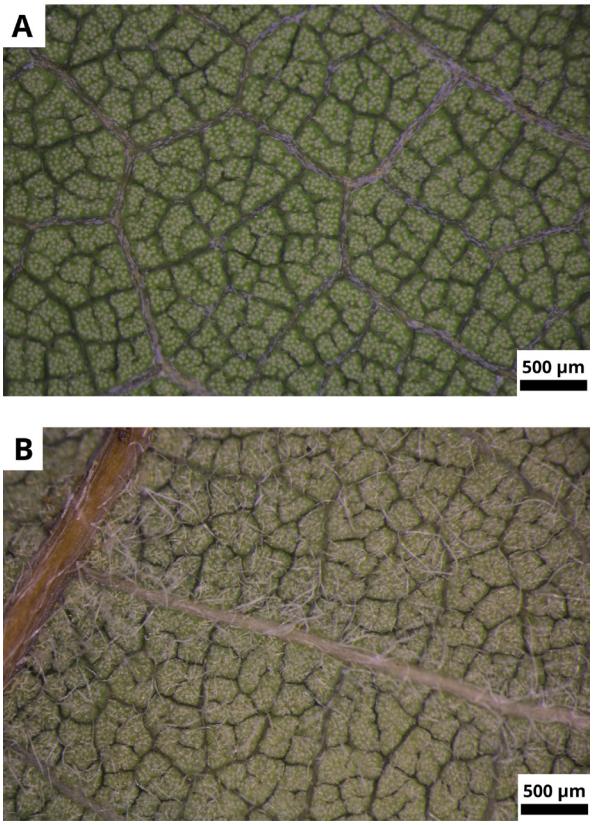


Fig. 3. Exemplary image of 5× magnified abaxial surface of a studied leaf: (A) individual K4507 (*Quercus robur* L.), (B) individual K4469 (*Quercus pedunculiflora* K. Koch).

ence in length between the two species ($N_{Q.robur}$ = 12,433, $N_{Q.pedunculiflora}$ = 23,301) proved to be normally distributed (Shapiro-Wilk-test: $p < 0.001$) and statistically significant (Student's t-test: $t = 55.902$; $p < 0.0001$). Fasciculate trichomes on greyish oak were present only on and along the veins, with one or two rays of an average length of 274.99 µm. Stellate trichomes were characterised by 2–4 short arms with an average length of 149.55 µm. Descriptive statistics of the observed trichome types are presented in Annex 1.

Trichome density showed remarkable differences (Table 1): pedunculate oak displayed significantly less trichome density compared to greyish oak (Shapiro–Wilk-test: $p < 0.05$; Student's t-test: $t = 7.799$, $p < 0.0001$) (Fig. 5). Interestingly, two *Quercus pedunculiflora* K. Koch individuals (K4463 and K4467) displayed exceptionally high trichome density values, which was attributable to the presence of a trichome type not found in other instances. This atypical trichome was described by Tschan & Denkt (2012) as fasciculate hair without a prominent pedestal branching above the epidermis on the entire leaf surface and has not been recorded in our taxa and was only reported from (sub-)Mediterranean oaks (*Q. pubescens* Willd., *Q. infectoria* subsp. *veneris* [A. Kern.] Meikle). The above two individuals with the atypical trichomes were excluded from the analyses as outliers. An additional remarkable outlier among the pedunculate oak samples was sample K4509, which displayed a high trichome density (213 trichomes/mm^2). This sample, collected in "Nagyerdő" Forest of Debrecen (E Hungary), possessed stellate trichomes – otherwise only found on greyish oak in our study – with a length of trichome rays from 52.57 µm to 242.75 µm.

Interestingly, we observed an intriguing difference between the lengths of trichomes within the studied pedunculate oak populations (Fig. 6). The two *Quercus robur* L. populations from Hungary (Debrecen and Kunpeszér) displayed the shortest trichome ray length (63.5 µm and 65 µm, respectively). Two Bulgarian populations (Bivolare & Riben and Pleven) with a mean ray length of 73.5 µm and 75 µm, respectively, are somehow intermediate to the other populations including a pedunculate oak from Romania (Piscul Sadoveii).

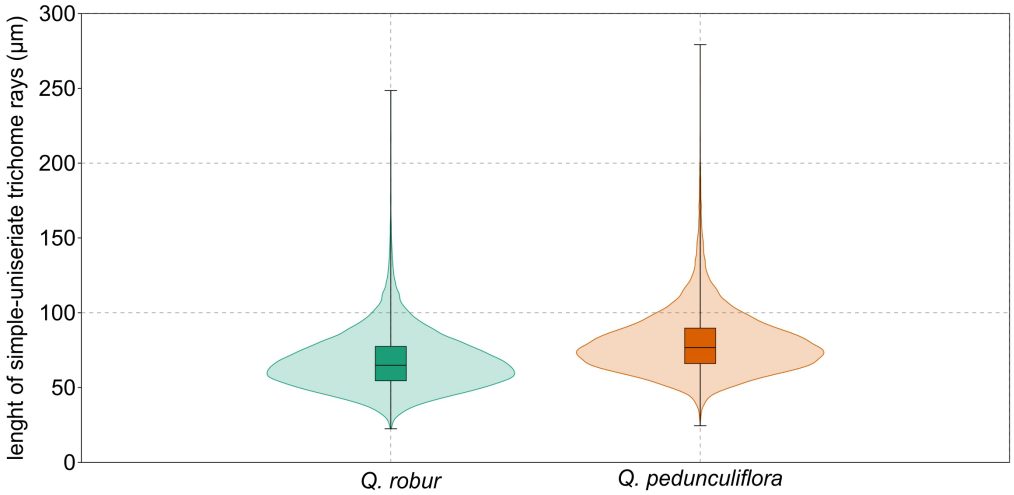


Fig. 4. Comparison of glandular and simple-uniseriate trichome rays of *Quercus robur* L. and *Quercus pedunculiflora* K. Koch presented as a combined violin and box plot. (Whiskers indicate minimum and maximum values, the median is shown in the middle of the box, the top of the box indicates the upper quartile, and the bottom line of the box indicates the lower quartile).

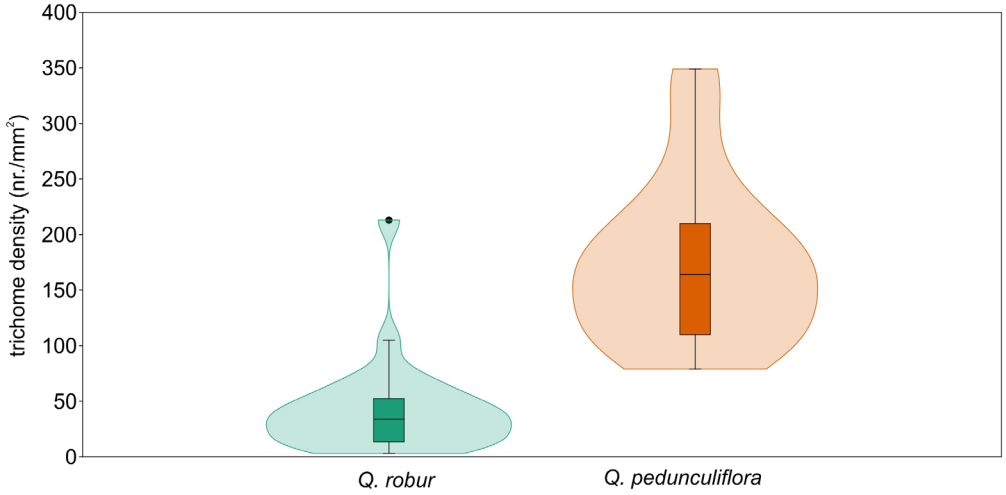


Fig. 5. Comparison of trichome densities of pedunculate and greyish oak displayed as combined violin and box plots. (Whiskers represent the minimum and maximum values, the median is shown in the middle of the box, the top of the box is the upper quartile, the bottom line of the box is the lower quartile, the point represents the outlier).

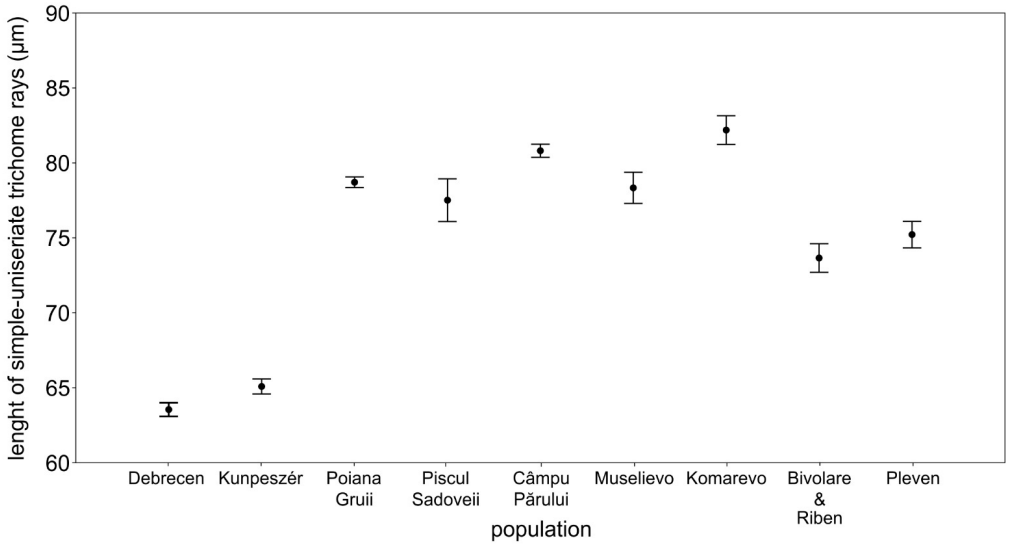


Fig. 6. Univariate distribution of the lengths of the glandular and simple-uniseriate trichome rays by population. Note: Dots denote means, while whiskers stand for the standard error.

4. Discussion

4.1. Comparative trichome morphology

Based on the results of our study, *Quercus robur* L. and *Q. pedunculiflora* K. Koch can be distinguished based on abaxial leaf indumentum: pedunculate oak has fewer hairs and can be characterised by a single hair type, whereas greyish oak displays higher trichome density and diversity. These characteristics explain the observation of Curtu et al. (2011) who found – without specifying the trichome types – the abaxial morphology to be distinctive in the two species. Later, Romanian researchers highlighted valuable differences in indumentum type (Apostol et al. 2017; Enescu 2017; Apostol 2019), we attempted here to provide a comprehensive comparison of trichome types of these two taxa.

Longer simple-uniseriate trichome rays and two more trichome types were observed on the abaxial leaf surface of greyish oak compared to pedunculate oak. The literature commonly reports three types of trichomes from *Q. pedunculiflora* K. Koch although with different ray lengths. Observations from Iran described stellate trichome with 2–4-rays on greyish oak with 60–130 µm lengths (Panahi et al. 2012). In addition to the stellate trichomes, short simple-uniseriate trichomes with 80–115 µm lengths were observed and no fasciculate trichomes were found (Panahi et al. 2012). Uzunova

& Palamarev (1992) identified three trichome types with the following results according to trichome type: simple-uniseriate trichome length was 120–150 µm, stellate trichome was 60–150 µm and fasciculate trichome was 250–350 µm. In our previous study on greyish oak (Hegedüs et al. 2023), it was observed that both stellate and fasciculate trichomes in addition to simple-uniseriate trichomes, whereas on *Q. robur* L. we found only simple-uniseriate trichome with 19.0–98.6 µm length.

Because of its large acreage and economic importance, several researchers in Europe have studied the leaf morphology and indumentum of pedunculate oak in more detail (e.g., Schwarz 1937; Bussotti & Grossoni 1997; Aas 1998). Bussotti & Grossoni (1997) observed 50–150 µm long simple-uniseriate trichomes, Gellini et al. (1992) and Mehrina et al. (2013) report hairless adaxial surface and the presence of simple-uniseriate trichome on the abaxial side. In his study, Aas (1998) placed the length of the trichome rays between 50–120 µm and observed that they could be up to 180 µm long. A similar result was obtained by Uzunova & Palamarev (1992), who found simple-uniseriate trichomes of 80–100 µm in length and 9 µm in diameter.

These differences in length of different trichome types within the same species between different studies may simply reflect intra-specific morphological variation of both species. Similarly large variation was reported in a meta-analysis of *Quercus* subsect. *Galliferae* by Tschan & Denkt (2012) and can reflect adaptation to local eco-geographical conditions (Meger et al. 2024), although we cannot rule out the effect of different measurement methodology as the reason behind the differences. Nevertheless, the marked qualitative differences in abaxial leaf morphology between the two taxa reported here and elsewhere in the literature serves as a strong basis for distinguishing between the two taxa, *Q. robur* L. and *Q. pedunculiflora* K. Koch.

4.2. Trichome characteristics and drought tolerance

Greyish oak was found to display higher trichome density and variability compared to pedunculate oak, which may reflect to a better drought-tolerance. Observations in the forest-steppe areas east and south of the Carpathians in Romania suggest that these two taxa are ecologically vicariants: *Quercus robur* L. prefers more humid stands, whereas *Q. pedunculiflora* K. Koch is a typical forest-steppe taxon (Georgescu & Morariu 1948; Apostol et al. 2017). The ecological preference of greyish oak to dryer areas were also noted by Curtu et al. (2011), who reported the dominance of this species in areas that are no longer ecologically tolerable for pedunculate oak in Romania. An experiment in Türkiye investigated the limits of the distribution of pedunculate oak and greyish oak as a function of bioclimatic factors (Yilmaz et al. 2016). They concluded that greyish oak has a higher tolerance to extreme climatic factors than pedunculate oak, which can be the reason behind the prevailing presence of greyish oak east of the Anatolian diagonal (Uslu et al. 2011).

Distribution of the two taxa shows a large overlap in South-Eastern Europe and Asia Minor (Jalas & Suominen 1976; Uslu et al. 2011), but they are apparently mutually vicariant at two habitat types: pedunculate oak is present in wetter habitats with good reach to ground water, while the more drought-tolerant greyish oak is present in drier habitats. This differentiation along a hydrological gradient is also visible in our sample set: if we only consider our a posteriori taxonomic classification, all *Q. robur* L. localities in Romania and Bulgaria are confined to riparian mixed forests along rivers (e.g., Olt River in Romania, Vit River in Bulgaria) or the territory of settlements (e.g., Muselievo, Pleven). Therefore, if the observed ecological preferences are consistently stable between these taxa and if persistent gene flow can be empirically validated, then the possibility of considering their taxonomic status as ecotypes of a single species raises and warrants further investigation.

Remarkably, the genetic analyses presented by Curtu et al. (2011) found no genetic differences between the two taxa that aligns well with our above statement. However, an answer for this taxonomic question needs additional genetic work preferably using a genomic approach that could answer questions of adaptation to local hydrological conditions. Recent phylogenomic study and ecological niche modelling have observed that some taxa have shifted towards being more tolerant regarding summer drought. One of these taxa is the greyish oak (Martín-Sánchez et al. 2024b).

4.3. Presence of indumentum morphotypes

In the remnant forest-steppe oakwood of "Peszér Forest", a habitat of notable naturalness because of minimal anthropogenic disturbance and ecological continuity (Molnár et al. 2022), we hypothesized the presence of *Quercus pedunculiflora* K. Koch. However, trichome analysis of specimens a priori classified as *Q. pedunculiflora* K. Koch revealed the presence of only glandular and simple-uniseriate structures, which contrast with the stellate and fasciculate trichomes documented in southern Romanian populations of this species (Table 1). This trait instead aligns with diagnostic features of *Quercus robur* L. (Table 1), leading us to reclassify all specimens from this forest a posteriori as *Q. robur* L.

In contrast, on the abaxial leaf surface of specimen K4509 from Debrecen, which was identified as pedunculate oak, the presence of stellate trichome was observed. By considering the opinion of Gencsi & Vancsura (1992), who presumed the presence of greyish oak in Eastern

Hungary, we may hypothesise the potential role of gene flow from greyish oak via hybridisation for this observation. The "Nyírség" region of Northeast Hungary once hosted extensive stands of sandy oak forests and forest-steppe flora connected to such dry woods (Kerner 1863). Unfortunately, this large geographical region has been greatly transformed by recent forestry practice that prefers *Robinia pseudoacacia* L. over to native oak forests. However, if greyish oak had been present in the region, it could leave its genetic material on specimen K4509, which can show the result of introgression from greyish oak.

Hybridization in European oaks is widespread and observed between several species (Petit et al. 2002). In this respect, the presence of stellate trichomes in the Debrecen specimen can also be explained if we suppose hybridisation between *Q. robur* L. and *Q. pubescens* Willd. (Kézdy 2001). Nevertheless, Curtu et al. (2007) studied a mixed oak stand and based solely on leaf morphological traits, 94% of all individuals were identified as "pure" species and only 6% was considered as hybrid. Similarly, Apostol et al. (2017) evidenced hybridisation between the two species, reflected in traits like leaf color, in only certain populations. However, genetic results (Curtu et al. 2011; Zimmermann et al. 2025) do not support this observation, and they suggest large-scale hybridisation among white oaks (sect. *Quercus*). This feature of white oaks can be beneficial, since such gene flow can potentially be used to improve some traits such as drought-tolerance (Mátyás 2002). Evidently, the potential gene flow between pedunculate and greyish oak should be studied further with the powerful toolkit of forest genomics (Neale & Kremer 2011).

The denser, more complex indumentum of *Q. pedunculiflora* K. Koch likely reflects an adaptation to aridity, making it a promising candidate for assisted gene flow (Kurz et al. 2023) to enhance drought resilience in *Q. robur* L. populations, particularly as climate projections predict intensifying summer droughts in Central-Eastern Europe (Bartholy et al. 2014). Two potential strategies for implementing this approach are: (1) introducing selected individuals into existing *Quercus robur* L. stands, or (2) establishing new *Quercus pedunculiflora* K. Koch stands adjacent to *Q. robur* L. forests. We must stress that prior to any intervention involving genetic manipulation of native forests, a comprehensive understanding of the genetic basis of adaptive traits, facilitated by forest genomics, is imperative. Furthermore, these strategies must account for the distinct ecological preferences of each taxon. Considering the comparable ecological functions of *Q. pedunculiflora* K. Koch and *Q. robur* L. woodlands (Doniță et al. 2003), the latter strategy appears more advantageous: establishing *Q. pedunculiflora* K. Koch stands in suitable ecological conditions near *Q. robur* L. forests could promote assisted gene flow to *Q. robur* L. and facilitate the potential migration of local forest biodiversity to more drought-tolerant habitats that provide similar ecological functions.

5. Conclusions

This study characterizes specific differences in abaxial leaf indumentum between *Quercus robur* L. and *Q. pedunculiflora* K. Koch. Specifically, fasciculate trichomes are diagnostic for *Q. pedunculiflora* K. Koch, even when stellate trichomes occur in individuals exhibiting intermediate morphology. These traits provide a practical tool for species identification in forestry, despite occasional phenotypic overlap. The observed trichome characteristics align with ecological preferences, reflecting that *Q. pedunculiflora* K. Koch is more drought-tolerant. This suggests the potential for assisted gene flow to enhance drought resilience in *Q. robur* L. populations in the face of climate change. Additionally, given the similar ecological function of these keystone species, the more drought-tolerant taxon can be regarded as a suitable candidate for afforestation in appropriate habitats in climate-smart and nature conservation-friendly forestry practice. Ultimately, understanding and leveraging the subtle morphological adaptations of these oak species is crucial for ensuring the resilience and sustainability of Central European oak forests in a rapidly changing climate.

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Annexes

Annex 1. Descriptive statistics of individuals by trichome type.

Trichome type	Identification code	K4438	K4439	K4440	K4441	K4442	K4443	K4444	K4445	K4446	K4447	K4448	K4449
Glandular, simple-uniseriate trichome	Mean (µm)	55.20	86.69	87.50	73.32	84.73	78.03	73.87	80.69	79.99	74.65	74.53	77.83
	Std. dev. (µm)	12.97	22.73	15.43	14.09	16.52	15.50	15.10	15.15	21.09	12.53	18.70	17.48
	Minimum (µm)	29.65	31.85	45.79	38.27	49.20	40.32	45.44	48.65	32.75	40.56	34.56	37.27
	Maximum (µm)	134.23	248.53	158.99	132.46	169.52	131.67	125.78	161.94	177.30	129.74	201.44	149.23
	Median (µm)	52.45	87.35	87.22	73.78	78.94	75.59	72.31	79.17	71.49	73.54	71.18	76.98
Stellate trichome	Mean (µm)	—	—	134.92	114.23	171.01	139.66	140.88	—	—	—	—	—
	Std. dev. (µm)	—	—	37.20	49.07	40.55	51.59	34.40	—	—	—	—	—
	Minimum (µm)	—	—	69.78	47.94	74.64	65.96	78.20	—	—	—	—	—
	Maximum (µm)	—	—	339.56	447.99	319.88	483.87	324.81	—	—	—	—	—
	Median (µm)	—	—	125.50	99.00	166.06	123.80	134.83	—	—	—	—	—
Fasciculate trichome	Mean (µm)	—	—	282.08	436.69	—	404.62	400.24	—	—	—	—	—
	Std. dev. (µm)	—	—	61.89	124.27	—	85.72	86.82	—	—	—	—	—
	Minimum (µm)	—	—	143.96	183.71	—	170.77	295.35	—	—	—	—	—
	Maximum (µm)	—	—	471.13	767.28	—	694.12	516.57	—	—	—	—	—
	Median (µm)	—	—	280.77	429.41	—	310.67	411.60	—	—	—	—	—

Trichome type	Identification code	K4450	K4451	K4452	K4453	K4454	K4455	K4456	K4457	K4458	K4459	K4460	K4461
Glandular, simple-uniseriate trichome	Mean (µm)	69.59	80.78	79.57	80.18	78.35	75.04	77.73	87.80	79.56	79.39	76.12	82.41
	Std. dev. (µm)	13.59	16.92	20.24	18.82	16.31	16.56	15.53	19.49	16.99	15.91	15.45	14.14
	Minimum (µm)	31.31	27.37	36.08	37.27	34.72	30.24	37.55	44.25	30.80	34.98	30.32	41.01
	Maximum (µm)	128.96	165.93	208.27	150.15	153.90	158.94	150.81	255.93	156.68	152.04	156.12	151.25
	Median (µm)	68.66	76.53	75.96	76.64	79.15	74.77	75.49	85.12	77.28	79.66	72.90	81.32
Stellate trichome	Mean (µm)	163.92	235.34	139.76	159.02	151.67	151.08	131.56	131.96	127.95	165.55	131.23	178.63
	Std. dev. (µm)	55.55	60.53	43.10	44.78	52.97	66.81	34.97	33.07	39.18	71.81	32.76	75.08
	Minimum (µm)	103.92	98.29	74.88	70.58	54.15	68.43	63.10	68.47	55.74	59.85	59.31	66.13
	Maximum (µm)	244.12	558.32	372.19	365.79	430.82	704.20	294.27	311.35	348.10	530.83	335.63	741.75
	Median (µm)	147.27	232.23	129.95	154.62	134.22	124.23	124.70	124.04	115.44	146.93	128.53	156.57
Fasciculate trichome	Mean (µm)	394.01	—	245.54	—	315.04	479.32	387.84	272.72	356.17	448.20	262.30	459.76
	Std. dev. (µm)	95.32	—	47.41	—	98.96	161.18	112.91	61.23	100.49	86.76	48.20	91.48
	Minimum (µm)	257.57	—	173.84	—	159.98	208.70	167.85	160.54	205.95	256.44	150.84	255.49
	Maximum (µm)	559.39	—	316.00	—	784.45	1,225.83	772.54	380.69	646.98	701.28	417.60	745.44
	Median (µm)	372.94	—	262.95	—	295.32	422.90	369.88	285.61	342.80	449.02	244.20	468.57

Trichome type	Identification code	K4462	K4464	K4465	K4466	K4468	K4469	K4470	K4495	K4496	K4497	K4498	K4499
Glandular, simple-uniseriate trichome	Mean (µm)	78.66	124.06	90.00	87.43	79.83	78.30	65.02	72.17	45.24	55.45	65.91	56.82
	Std. dev. (µm)	14.75	26.41	18.91	18.97	23.91	15.20	10.79	17.70	13.87	11.94	16.60	13.46
	Minimum (µm)	39.48	53.69	35.74	47.94	24.51	33.63	37.06	25.17	22.47	25.03	24.34	23.52
	Maximum (µm)	142.70	279.18	217.13	182.75	190.44	152.22	120.48	160.24	86.74	112.83	129.93	139.13
	Median (µm)	78.56	132.25	87.19	84.17	74.62	76.64	65.39	68.73	38.35	55.17	64.88	53.18
Stellate trichome	Mean (µm)	150.15	178.18	152.18	168.95	190.96	215.65	134.91	—	—	—	—	—
	Std. dev. (µm)	39.88	47.62	45.40	61.51	80.10	80.41	39.35	—	—	—	—	—
	Minimum (µm)	67.61	91.40	62.34	69.91	76.14	80.15	57.17	—	—	—	—	—
	Maximum (µm)	381.95	472.82	391.19	585.43	599.78	590.14	400.92	—	—	—	—	—
	Median (µm)	144.17	167.42	138.96	152.79	169.54	196.31	125.45	—	—	—	—	—
Fasciculate trichome	Mean (µm)	387.71	370.40	326.91	395.91	432.30	384.97	298.58	—	—	—	—	—
	Std. dev. (µm)	72.47	95.72	68.86	78.25	113.14	71.98	80.03	—	—	—	—	—
	Minimum (µm)	243.93	218.39	195.15	266.54	259.55	182.26	67.51	—	—	—	—	—
	Maximum (µm)	543.85	575.23	504.11	642.11	813.64	721.36	588.61	—	—	—	—	—
	Median (µm)	392.53	370.97	296.59	396.38	401.71	332.74	315.52	—	—	—	—	—

Trichome type	Identification code	K4500	K4501	K4502	K4503	K4504	K4505	K4506	K4507	K4508	K4509	K4510	K4511	K4512
Glandular, simple-uniseriate trichome	Mean (µm)	67.08	84.22	72.03	77.62	55.51	56.36	66.56	67.16	67.12	60.95	60.08	70.04	57.97
	Std. dev. (µm)	16.49	32.38	17.38	20.26	14.17	10.54	15.46	12.43	12.67	12.19	13.41	2.40	10.45
	Minimum (µm)	25.82	29.37	30.08	27.53	23.75	28.37	39.14	37.12	38.48	31.01	30.32	39.15	27.12
	Maximum (µm)	161.38	217.77	144.61	176.86	137.61	102.96	135.37	127.02	143.17	123.93	121.20	134.84	109.54
	Median (µm)	65.26	75.66	73.08	75.70	56.34	52.94	64.90	65.65	65.27	59.67	54.65	69.88	56.73
Stellate trichome	Mean (µm)	—	—	—	—	—	—	—	—	—	109.53	—	—	—
	Std. Dev. (µm)	—	—	—	—	—	—	—	—	—	22.20	—	—	—
	Minimum (µm)	—	—	—	—	—	—	—	—	—	52.57	—	—	—
	Maximum (µm)	—	—	—	—	—	—	—	—	—	242.75	—	—	—
	Median (µm)	—	—	—	—	—	—	—	—	—	108.06	—	—	—
Fasciculate trichome	Mean (µm)	—	—	—	—	—	—	—	—	—	—	—	—	—
	Std. dev. (µm)	—	—	—	—	—	—	—	—	—	—	—	—	—
	Minimum (µm)	—	—	—	—	—	—	—	—	—	—	—	—	—
	Maximum (µm)	—	—	—	—	—	—	—	—	—	—	—	—	—
	Median (µm)	—	—	—	—	—	—	—	—	—	—	—	—	—