UDC 582.632.2:615:322:615.072:54.061/.062:547.9:577.15/.17

Tetiana OMELKOVETS
Senior Lecturer of the Department of Pharmaceutical and Biological Chemistry, Pharmacognosy, PHEE "Kyiv Medical University", Boryspilska str., 2, Kyiv, Ukraine, 02099 (t.omelkovets@kmu.edu.ua)
***ORCID:** 0000-0002-1730-1630*
***SCOPUS:** 58248664300*

Olena KONOVALOVA
Doctor of Pharmaceutical Sciences, Professor and Head of the Department of Pharmaceutical and Biological Chemistry, Pharmacognosy PHEE "Kyiv Medical University", Boryspilska str., 2, Kyiv, Ukraine, 02099 (o.konovalova@kmu.edu.ua)
***ORCID:** 0000-0001-6025-5230*
***SCOPUS:** 6508198095; 57552970200*
***RESEARCHER ID:** CAH-7409-2022*

Olha SHCHERBAKOVA
Candidate of Biological Sciences, Senior Research Associate of the Department of Botany, National Museum of Natural History of NAS of Ukraine, Bohdana Khmelnytskoho str., 15, Kyiv, Ukraine 01054; Associate Professor of the Department of Pharmaceutical and Biological Chemistry, Pharmacognosy, PHEE "Kyiv Medical University", Boryspilska str., 2, Kyiv, Ukraine, 02099 (o.shcherbakova@kmu.edu.ua)
***ORCID:** 0000-0001-6601-6476*
***SCOPUS:** 58250303800*

Mariia KALISTA
Candidate of Biological Sciences, Research Associate of the Department of Botany, National Museum of Natural History of NAS of Ukraine, Bohdana Khmelnytskoho str., 15, Kyiv, Ukraine 01054; Associate Professor of the Department of Pharmaceutical and Biological Chemistry, Pharmacognosy, PHEE "Kyiv Medical University", Boryspilska str., 2, Kyiv, Ukraine, 02099 (m.kalista@kmu.edu.ua)
***ORCID**: 0000-0002-2335-5184*
***SCOPUS:** 57193743485*
***RESEARCHER ID:** HNB-9659-2023*

Iryna HURTOVETKO
Candidate of Pharmaceutical Sciences, Associate Professor of the Department of Pharmaceutical and Biological Chemistry, Pharmacognosy, PHEE «Kyiv Medical University», Boryspilska str., 2, Kyiv, Ukraine, 02099 (i.hurtovenko@kmu.edu.ua)
***ORCID:** 0000-0003-2442-3406*
***SCOPUS:** 57552046000*

Kateryna NOVOSAD
Candidate of Biological Sciences, Research Associate of the Department of Botany, National Museum of Natural History of NAS of Ukraine, Bohdana Khmelnytskoho str., 15, Kyiv, Ukraine, 01054 (novosad-katya@ukr.net)
***ORCID:** 0000-0002-6704-0336*

To cite this article: Omelkovets T., Konovalova O., Shcherbakova O., Kalista M., Hurtovenko I., Novosad K. (2024). Comparative anatomical study of *Quercus robur* L. and *Quercus rubra* L. leaves structure and identification of diagnostic features for standardization and quality control of medicinal plant raw materials. *Fitoterapiia. Chasopys – Phytotherapy. Journal*, 3, 138–161, doi: https://doi.org/10.32782/2522-9680-2024-3-138

COMPARATIVE ANATOMICAL STUDY OF *QUERCUS ROBUR* L. AND *QUERCUS RUBRA* L. LEAVES STRUCTURE AND IDENTIFICATION OF DIAGNOSTIC FEATURES FOR STANDARDIZATION AND QUALITY CONTROL OF MEDICINAL PLANT RAW MATERIALS

Actuality. *An important stage of pharmacognostic analysis of medicinal plants is the morphological and anatomical research, which solves the task of searching the diagnostic features for species identification, which provides guarantees when identifying the identity and quality of medicinal plant raw materials.*

The aim of the work was *to identify the diagnostic features of Quercus robur L. and Quercus rubra L. leaves structure on the basis of a comparative anatomical and morphological study.*

Material and methods. *For anatomical studies fragments of the leaf blade 2×2 cm in size, taken from its middle part, were used. All samples were photographed under a light microscope (SUNNY XSM-20 6,500) using a Sigeta MCMOS 5100 5.1 MP digital camera. Anatomical linear measurements were made using Image J software (NIH, Wayne Rasband; http://rsbweb.nih.gov/ij/). The samples for morphometric measurements were at least 25 values. Statistical processing of the measurement results was carried out in the program Statistica (Data Analysis Software System), V.6 software; arithmetic mean (M) and standard deviation (±SD) were calculated for anatomometric indicators.*

Research results. *The results of the research made it possible to identify the anatomical characteristics of the leaf blade and petiole of Q. rubra and Q. robur, which have diagnostic value and can be used to identify medicinal raw materials of these species. It is shown that the following are of the greatest diagnostic significance: the nature of pubescence of leaves, midribs and petioles, quantitative indicators and the nature of the distribution of crystalline inclusions in different parts of leaves, features of the structure of the vascular system of the midrib and petiole. Most of the dimensional indicators of the anatomical structure of the leaf plate varied in both species and cannot be used as reliable in the identification of raw materials.*

Conclusion. *According to the results of the current study, it was found out that the leaves of Q. rubra and Q. robur are a promising objects for pharmacognostic study and introduction into official medicine. In this study, the qualitative and quantitative variability of the anatomical features of the structure of the leaf plate of Q. rubra compared to Q. robur and the possibility of their use for identifying the identity, standardization and quality control of medicinal plant raw materials were determined.*

Key words: *red oak, common oak, Quercus rubra, Quercus robur, leaves, anatomometric indicators, microdiagnostics of raw materials.*

Тетяна ОМЕЛЬКОВЕЦЬ
старший викладач кафедри фармацевтичної і біологічної хімії, фармакогнозії, ПВНЗ «Київський медичний університет», вул. Бориспільська, 2, м. Київ, Україна, 02099 (t.omelkovets@kmu.edu.ua)
ORCID: *0000-0002-1730-1630*
SCOPUS: *58248664300*

Олена КОНОВАЛОВА
доктор фармацевтичних наук, професор, завідувач кафедри фармацевтичної і біологічної хімії, фармакогнозії, ПВНЗ «Київський медичний університет», вул. Бориспільська, 2, м. Київ, Україна, 02099 (o.konovalova@kmu.edu.ua)
ORCID: *0000-0001-6025-5230*
SCOPUS: *6508198095; 57552970200*
RESEARCHER ID: *CAH-7409-2022*

Ольга ЩЕРБАКОВА
кандидат біологічних наук, старший науковий співробітник відділу ботаніки, Національний науково-природничий музей НАН України, вул. Богдана Хмельницького, 15, м. Київ, Україна, 01601; доцент кафедри фармацевтичної і біологічної хімії, фармакогнозії, ПВНЗ «Київський медичний університет», вул. Бориспільська, 2, м. Київ, Україна, 02099 (o.shcherbakova@kmu.edu.ua)
ORCID: *0000-0001-6601-6476*
SCOPUS: *58250303800*

Марія КАЛІСТА
кандидат біологічних наук, науковий співробітник відділу ботаніки, Національний науково-природничий музей НАН України, вул. Богдана Хмельницького, 15, м. Київ, Україна, 01054; доцент кафедри фармацевтичної і біологічної хімії, фармакогнозії, ПВНЗ «Київський медичний університет» вул. Бориспільська, 2, м. Київ, Україна, 02099 (m.kalista@kmu.edu.ua)
ORCID: *0000-0002-2335-5184*
SCOPUS: *57193743485*
RESEARCHER ID: *HNB-9659-2023*

Ірина ГУРТОВЕНКО
кандидат фармацевтичних наук, доцент кафедри фармацевтичної і біологічної хімії, фармакогнозії, ПВНЗ «Київський медичний університет», вул. Бориспільська, 2, м. Київ, Україна, 02099 (i.hurtovenko@kmu.edu.ua)
ORCID: *0000-0003-2442-3406*
SCOPUS: *57552046000*

Катерина НОВОСАД
кандидат біологічних наук, науковий співробітник відділу ботаніки, Національний науково-природничий музей НАН України, вул. Богдана Хмельницького, 15, м. Київ, Україна, 01054 (novosad-katya@ukr.net)
ORCID: *0000-0002-6704-0336*

Бібліографічний опис статті: Омельковець Т., Коновалова О., Щербакова О., Каліста М., Гуртовенко І., Новосад К. (2024). Порівняльно-анатомічне вивчення будови листків *Quercus robur* L. і *Quercus rubra* L. та виявлення діагностичних ознак для стандартизації та контролю якості лікарської рослинної сировини. *Фітотерапія. Часопис*, 3, 138–161, doi: https://doi.org/10.32782/2522-9680-2024-3-138

ПОРІВНЯЛЬНО-АНАТОМІЧНЕ ВИВЧЕННЯ БУДОВИ ЛИСТКІВ *QUERCUS ROBUR* L. І *QUERCUS RUBRA* L. ТА ВИЯВЛЕННЯ ДІАГНОСТИЧНИХ ОЗНАК ДЛЯ СТАНДАРТИЗАЦІЇ ТА КОНТРОЛЮ ЯКОСТІ ЛІКАРСЬКОЇ РОСЛИННОЇ СИРОВИНИ

Актуальність. *Важливим етапом фармакогностичного аналізу лікарських рослин є морфолого-анатомічні дослідження, які вирішують завдання пошуку діагностичних ознак для видової ідентифікації, що надає гарантії під час установлення тотожності та якості лікарської сировини.*

Мета дослідження. *Установлення відмітних діагностичних ознак будови листків Quercus robur L. та Quercus rubra L. на основі порівняльного анатомо-морфологічного дослідження.*

Матеріал і методи. *Об'єктами дослідження були зразки листків Q. rubra та Q. robur, зібрані у вересні 2023 р. на території Національного ботанічного саду імені М. М. Гришка. Для анатомічних досліджень використовували фрагменти листкової пластинки розміром 2×2 см, узяті з її середньої частини. Усі зразки були сфотографовані під світловим мікроскопом (SUNNY XSM-20 6 500) за допомогою цифрової камери Sigeta MCMOS 5100 5.1 MP. Анатомічні лінійні вимірювання проводили за допомогою програмного забезпечення Image J (NIH, Wayne Rasband; http://rsbweb.nih.gov/ij/). Статистична обробка результатів вимірювання проводилася у програмі Statistica (Data Analysis Software System), V.6 software; для анатомо-метричних показників були розраховані середнє арифметичне (M) та стандартне (±SD) відхилення.*

Результати дослідження. *Результати досліджень дали змогу виділити анатомічні характеристики листкової пластинки і черешка Q. rubra та Q. robur, які мають діагностичну цінність і можуть бути використані для ідентифікації лікарської сировини цих видів. Показано, що найбільшу діагностичну значимість мають: характер опушення листків, середніх жилок і черешків, кількісні показники та характер розподілу кристалічних включень у різних частинах листків, особливості будови провідної системи середньої жилки та черешка. Більшість розмірних показників анатомічної будови листкової пластинки варіюють у обох видів і не можуть бути використані як надійні під час ідентифікації сировини.*

Висновок. *За результатами проведеного дослідження встановлено, що листки Q. rubra і Q. robur є перспективним об'єктом для фармакогностичного вивчення та впровадження в офіційну медицину. У даному дослідженні встановлено якісну і кількісну варібельність анатомічних ознак будови листкової пластинки Q. rubra порівняно з Q. robur та можливість їх використання для встановлення тотожності, проведення стандартизації і контролю якості лікарської рослинної сировини.*

Ключові слова: *дуб червоний, дуб звичайний, Quercus rubra, Quercus robur, листя, анатомометричні показники, мікродіагностика сировини.*

Introduction. The genus *Quercus* L. belongs to one of the most widespread genera in the Northern Hemisphere (Leiva & Díaz-Maqueda, 2016). Species of the genus, due to the high content of biologically active substances (BAS), have been used in folk and official medicine as plants with antioxidant, anti-inflammatory, antimicrobial, antitumor, hypoglycemic, hypocholesterolemic, antihypertensive pharmacological activities (Morales, 2021). Most of the pharmacological effects are caused by the presence and significant quantitative content of polyphenols, in particular, tannins, flavonoids, hydroxycinnamic and other phenolic acids, procyanidins, as well as to a lesser extent other secondary metabolites (organic acids, terpenoids, aliphatic alcohols, etc.) and primary metabolites (monosaccharides, fatty acids, amino acids), present in all parts of the plant (Didem Sohretoglu & Gülin Renda, 2020).

The main phenolic compounds found in the leaves of *Quercus species* (*Q. glauca* Thunb, *Q. incana* Bartram, *Q. ilex* L., *Q. mongolica* Fisch. ex Ledeb., *Q. salicina* Blume, *Q. petraea*, *Q. robur* L., *Q. rubra* L.) are phenolic acids, including hydroxycinnamic (gallic acid, ellagic acid, protocatechuic acid, gentisic acid, vanillic acid, chlorogenic acid, caffeic acid); flavonoids (rutin, quercetin, epicatechin, naringenin, hesperetin) (Burlacu, Nisca, Tanase, 2020; Konovalova et al., 2023). Aliphatic alcohols are represented by docosanol, tetracosanol, octadecanol, pentacosanol, hexacosanol and hexadecanol (Burlacu et al., 2020). Palmitic, stearic, oleic and linoleic acids were identified among fatty acids of *Quercus* species (Petrovic et al., 2004). The significant distribution of the native species *Q. robur* and the invasive North American *Q. rubra* in the forests and plantations of Europe provides available substantial reserves of their raw materials, and the species themselves are promising for comprehensive pharmacognostic research.

The official medicinal raw material of *Q. robur* in the European Pharmacopoeia (2022) and the State Pharmacopoeia of Ukraine (2014) is its bark. The bark of *Q. rubra* is currently not used in official medicine and is still poorly studied for its phytochemical composition; however, preliminary studies confirm the potential biological effect of its phenolic components with antioxidant and antimicrobial properties (Tanase et al., 2022). The leaves of *Q. robur* contain a wide range of BAS. In addition to tannins (Pérez et al., 2017), they contain

flavonoids (Basile et al., 2000; Likhanov et al., 2019), as well as sterols (Burlacu et al., 2020). 155 volatile substances were identified in the essential oil of *Q. robur* leaves; in particular, cadinane type sesquiterpenes, which exhibit antifungal and antibacterial properties (Engel, 1993; Plainfossé et al., 2018). Studies on the chemical composition of the epicuticular waxes of *Q. robur* leaves showed that its dominant component is tetracosanol (it contains about 40% of the wax), which is a systemic fungicide with a strong protective effect against pathogens of the vegetative organs of plants (Gülz & Müller, 1992; Gülz et al., 1994). Aliphatic alcohols of plant waxes can be used as emulsifiers, emollients and thickeners in food and personal care products; have antimicrobial and antitumor effects also (Volin, 2001; Hilmarsson et al., 2007). The leaves of *Q. rubra* accumulate a significant amount of tannins, the content and ratio of which can vary depending on climatic conditions, in particular, the content of condensed tannins in green leaves ranges from 29 to 89% of the total tannin content and 53–88% in fallen leaves. About 69% of hydrolyzed tannins with a predominant content of ellagotannins are found in the green leaves of *Q. rubra* (collected during the first week of September), the content of which decreases during the growing season to 11% (in leaves collected during the second week of October) (Top et al., 2017).

The above data on the chemical composition of the *Q. robur* and *Q. rubra* leaves emphasize the relevance of an in-depth and comprehensive study of the raw materials of these species. An important stage of pharmacognostic analysis of medicinal plants is the morphological and anatomical research, which solves the task of researching the diagnostic features for species identification, which provides guarantees in determining the identity and quality of medicinal raw materials.

A. Camus classified the genus *Quercus* s.l. mainly on the basis of the characteristics of leaves and fruits into two subgenera: Euquercus (*Quercus* s.s.) and Cyclobalanopsis, the latter combining species from South Asia (Nixon, 1993).

According to modern data the genus *Quercus* is also divided into 2 subgenera: *Quercus* (sections *Lobatae, Protobalanus, Ponticae, Virentes, Quercus*) – species with lobed leaves and Cerris (sections Cyclobalanopsis, Cerris, Ilex) – species with toothed leaves (Denk et al., 2017; Hipp et al., 2020). The greatest species diversity is observed in oaks of North America and South Asia (Denk et al., 2017; Hipp et al., 2020). *Q. robur* belongs to section *Quercus* (=subg. Lepidobalanus, white Oaks), which includes 146 species from North and Central America, Mexico, Western Eurasia, East Asia, and North Africa (Nixon & Muller 1997; Denk et al., 2017; Hipp et al., 2020). *Q. rubra* belongs to the section Lobatae (=subg. Erythrobalanus, red Oaks), which unites 124 species distributed in North, South and Central America, Mexico and Colombia (Jensen, 1997; Denk et al., 2017; Hipp et al., 2020). Both sections represent a New World clade comprising sections Lobatae and *Quercus* s.s. (Deng et al., 2013).

It is shown that in the genus *Quercus*, the most frequently used macromorphological characters, in particular the morphology of acorns and leaves, do not always have taxonomic value, especially when identifying hybrids (Dupouey & Badeau, 1993; Rafii et al., 1993; Penas et al., 1994; Schicchi et al., 2001; Río et al., 2014). This is due to significant variability in the structure of fruits, and especially leaves, depending on environmental factors, time of collection, location on the tree, degree of lightning, etc. (Jensen et al., 1993; Penas et al., 1994; Nikolić et al., 2005). Microscopic studies of species of the genus *Quercus* were primarily related to the search for diagnostic characters for the taxonomy of the genus.

The technology of scanning electron microscopy (SEM) has opened up new opportunities for detailed study and use in taxonomy, in particular representatives of the genus *Quercus*, features of the ultrastructure of the leaf surface, namely the nature of pubescence, the structure of the stomatal apparatus and epicuticular wax. Thanks to the detailing of the structure of trichomes under SEM and the improvement of their classification, it has become possible to use features of pubescence to identify not only species and hybrids of *Quercus*, but also subgenera and sections (Dyal, 1936; Hardin, 1976, 1979a; Thomson & Mohlenbrock, 1979; Jones, 1986; Kim et al., 1992; Penas et al., 1994; Llamas et al., 1995; Spellenberg & Bacon, 1996; Buck & Bidlack, 1998; Lou & Zhou, 2001; Ishida et al., 2003; Valencia & Delgado, 2003; Scareli-Santos et al., 2007; Panahi et al., 2012; Tschan & Denk, 2012; Deng et al., 2014; Uzunova et al., 1997, Fortini et al., 2009). The diagnostic value of trichome characters for the identification of *Q. robur* and *Q. rubra* has also been shown in a number of publications (Hardin, 1976, 1979 a,b; Bačlć, 1981; Penas et al., 1994; Bussotti & Grossoni, 1997; Fortini et al., 2009).

A study on seasonal patterns in leaf ontogeny showed that some of the trichomes present in young leaves are not preserved in mature leaves (Hardin, 1979b; Kim et al., 1992; Penas et al., 1994). Therefore, it is considered important to supplement SEM with light microscopy (LM), which better visualizes the bases remaining after trichome shedding (Deng et al., 2014). It was revealed that the development of dense leaf pubescence, which is characteristic of *Quercus* species, is protective not only against UV damage, but also against high insola-

tion (Karabourniotis et al., 1998). According to other data, trichomes may participate in cadmium detoxification (Choi et al., 2001). The various characteristics of the stomatal apparatus as diagnostic features include the shape, size, density of the guard cells, as well as the features of subsidiary cells were also used in the taxonomy of the genus *Quercus* (Bačlć, 1981; Gellini et al., 1992; Ashton & Berlyn, 1994; Bussotti & Grossoni, 1997; Lou & Zhou, 2001; Panahi et al., 2012). With the use of SEM, these studies were supplemented by the identification of diagnostic features of deposits of epicuticular waxes on the surface of leaves and especially on stomatal cells (Bussotti & Grossoni, 1997; Uzunova & Palamarev, 1993; Barthlott et al., 1998; Luo & Zhou, 2001; Scareli-Santos et al., 2007; Panahi et al., 2012). Currently, it remains relevant to study the composition and degree of development of epicuticular wax in different environmental conditions (Simões et al., 2020).

Another direction of numerous studies of the stomatal apparatus of *Quercus* developed in connection with determination of the correlation between various quantitative and qualitative changes with lighting conditions (Abrams & Kubiske, 1990; Nikolic et al., 2003; Batos et al., 2010; Daly & Gastaldo, 2010; Kryvoruchko & Bessonova, 2018) or the influence of anthropogenic factors (Mitrović et al., 1997; Kryvoruchko & Bessonova, 2017). It is revealed, for example, that there is an inverse relationship between the stomatal index of leaves and the concentration of CO2 in the environment, and the leaves of *Q. robur*, which are well preserved in sediments, can be an indicator of changes in the content of CO2 in the atmosphere during different geological epochs, in particular, its growth under the influence anthropogenic factors (Hoof et al., 2005).

A number of publications analyze the variability of morphological and anatomical features of the leaf structure in *Q. robur* (Dupouey, 1983; Borazan & Babaç, 2003; Nikolić et al., 2005; Boratynski et al., 2008; Kryvoruchko & Bessonova, 2017; Martins et al., 2022; Fortini et al., 2009) and *Q. rubra* (Abrams & Kubiske, 1990; Jensen et al., 1993; Ashton & Berlyn, 1994; Nagel et al., 1998; Kryvoruchko & Bessonova, 2017), which allows us to find out their adaptive mechanisms to different growth conditions (moisture, lighting, increased UV radiation, the influence of urbotechnogenic conditions). *Quercus* representatives have a leaf structure that corresponds to xerophytic species (Abrams & Kubiske, 1990). In particular, it was found out that under conditions of reduced insolation and in an urbotechnogenogenic environment, the histological parameters of *Q. robur* and *Q. rubra* leaves change equally towards xeromorphism, that is, there is a thickening of the cuticle and adaxial epiderma, an increase in the thickness of the palisade mesophyll and the density of stomata, and an increase in the palisade coefficient (Kryvoruchko & Bessonova, 2017, 2018).

Therefore, for the taxonomy of the genus *Quercus*, the importance of particular anatomical features of the structure of the leaves was shown and their variability in different environmental conditions was evaluated. There are no generalized data on clear diagnostic anatomical features of mature leaves of *Q. rubra* and *Q. robur* in the literature. Considering the fact that the leaves of both species are promising for use as medicinal raw materials, comprehensive comparative anatomical studies of these species are relevant.

The aim of the work was to identify the diagnostic features of the structure of *Quercus robur* and *Quercus rubra* leaves on the basis of a comparative anatomical and morphological study.

Materials and methods of the study. The samples of leaves of *Q. rubra* and *Q. robur* collected in September 2023 on the territory of the M.M. Gryshko National Botanical Garden of the National Academy of Sciences of Ukraine and were identified by O. Shcherbakova. The mature leaves were collected from the middle part of the annual growth of shoots, at a height of 2–2.5 m, under the same conditions of sufficient lighting. For anatomical studies fragments of the leaf blade 2×2 cm in size, taken from its middle part, were used. Samples for anatomical studies were fixed in 70% alcohol. The density of stomata was studied using the method of replicas (prints) (Meidner & Mansfield, 1968; Paul et al., 2017). To study the adaxial and abaxial epiderma of leaves, their segments were first boiled to remove epicuticular wax, then macerated, keeping in a 1:1 solution (by volume) of 10% H_2O_2 and 10% glacial acetic acid, heated to 60°C for no less than 24 hours or until the epiderma begins to separate (Deng et al., 2014; Matthew, 2022). After maceration, the upper and lower epiderma were separated with a needle and stained using a 0.1% (w/v) aqueous solution of safranin for 1 min, washed with 70% ethanol, then stained with 1% (w/v) aqueous Astra Blue solution for 10 min and washed with distilled water (Kraus et al., 1998). In the epidermal samples prepared in this way, the shape, size of epidermal cells and stomata, the nature of pubescence, and its density were studied using a light microscope. Transverse sections of leaf blades, midribs, and the medial part of petioles, which were made by hand with a razor, were painted in the same way.Also, for the analysis of pubescence of leaf blades, 1×1 cm leaf fragments were bleached in 5% sodium hypochlorite solution for better illumination (Hoof et al., 2005), then observed under a light microscope. All samples

were photographed under a light microscope (SUNNY XSM-20) using a Sigeta MCMOS 5100 5.1 MP digital camera.This study uses the classification and terminology of trichomes and their bases according to Deng et al. (2014), taking into account the works of J. W. Hardin (1976, 1979a, b) and J.H. Jones (1986).

Anatomical linear measurements were made using Image J software (NIH, Wayne Rasband; http://rsbweb.nih.gov/ij/). The samples for morphometric measurements were at least 25 values. Statistical processing of the measurement results was carried out in the program Statistica (Data Analysis Software System), V.6 software; arithmetic mean (M) and standard deviation (±SD) were calculated for anatomometric indicators.

Stomatal number (SN) or stomatal density (SD) was determined as the average number of stomata per 1 mm^2 of the surface area of the leaf epiderma (Evans, 2002; Hoof et al., 2005; Xavier et al., 2015).The stomatal index (SI) was defined as the percentage ratio of the number of stomata to the total number of stomata and other epidermal cells in the same area (SI) (%) = (S/S+E) × 100 where S and E are respectively the number of stomata and epidermal cells per unit area (or in the field of view of the microscope) (Evans, 2002; Hoof et al., 2005; Xavier et al., 2015; Paul et al., 2017). Xeromorphism index (%) = Ne+Nn / 100, where Ne is the density of epidermal cells, pcs./mm^2; Nn is the density of stomata, units/mm^2 (Kryvoruchko & Bessonova, 2018). The palisade coefficient was calculated as the ratio of the thickness of the palisade mesophyll of the leaf to the total thickness of the leaf and was expressed as a percentage. A palisade index of less than 30% is considered very low, 30 to 40% is low, 40 to 50% is medium, 50 to 60% is high, and more than 60% is very high. The palisade index is the most informative indicator that determines drought resistance, the higher this indicator, the more xeromorphic the leaf has (Kryvoruchko & Bessonova, 2017). For histochemical reactions, the following reagents were used to detect: lipophilic compounds – Sudan III (Foster, 1949); phenolic compounds – ferric chloride 2% (Johansen, 1940); lignified structures – phloroglucin/HCl (Sass, 1951); starch – Lugol's solution (Berlyn & Miksche, 1976).

Research results and their discussion. The leaves of *Q. rubra* and *Q. robur* are dorsiventral, hypostomous (the stomata are located only on the abaxial epiderma) (fig. 1: A.1, B.1; fig. 2: A.1, B.1). The upper and lower epiderma of the leaf is covered with a continuous layer of epicuticular wax, which in both species is epicuticular wax structure type platelets (Muhammada et al., 2020). Under SEM, numerous crystalloid plates with sharp fringed edges were noted on the upper and lower surfaces of the *Q. robur* leaf (Prasad & Gülz, 1990). On both the upper and lower side of the oak leaf, crystalloid platelets with sharp fringed edges were observed.

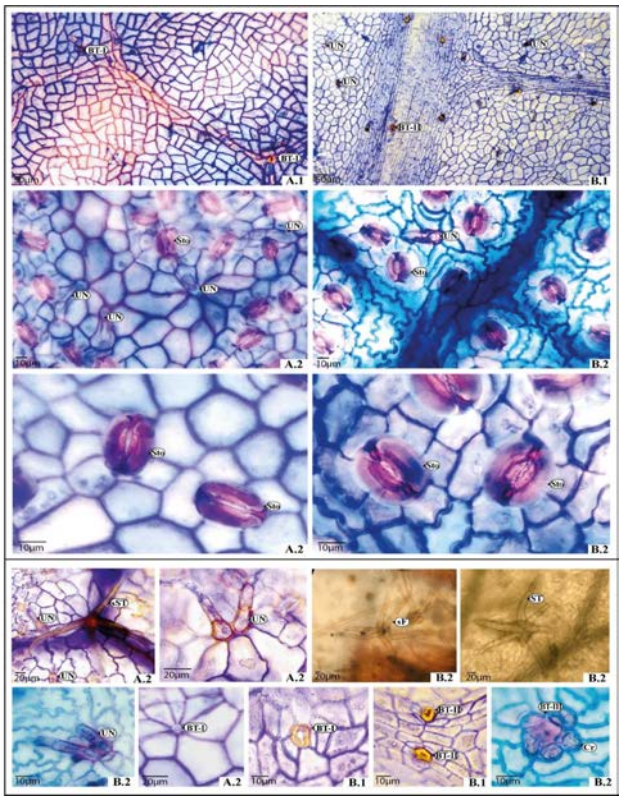

Fig 1. Anatomical structure of the leaf epiderma of: A. *Quercus robur*, B. *Quercus rubra*. 1. adaxial leaf epiderma; 2. abaxial leaf epiderma; Cr – calcium oxalate crystal; Sto – stomata. Trichomes: ST – stellate; sST – simplified stellate; sF – stipitate fasciculate; UN – uniseriate. Trichome bases: BT-I – the first type, BT-II – the second type, BT-III – the third type.

Adaxial epiderma. The epidermal cells of the adaxial surface of the leaves of both species have the shape of irregular quadrangles or polygons with straight to curved anticlinal walls. The length and width (L×W) of epidermal cells are slightly larger in *Q. rubra* (50.06±9.53×26.63±4.89) than in *Q. robur* (45.19±11.07×25.07±5.12); accordingly, the density of epidermal cells is lower in *Q. rubra* (1056.23±129.94) compared to Q. robur (1152.96±124.92) (table 1). Epidermal cells of both species have inclusions in the form of simple cubic crystals and druses. From the adaxial side, the crystal-bearing covering of large veins is clearly visible (fig. 2: B.2a).

Table 1

Anatomometric indicators of the *Quercus robur* and *Quercus rubra* leaf blade

Parameters		*Quercus robur*		*Quercus rubra*	
		Mean value	Range limit	Mean value	Range limit
The thickness of the leaf plate		179.64±10.29	141.21–205.77	146.11±6.12	121.10–198.41
Cells of the adaxial epiderma	length, μm	45.19±11.07	22.15–69.36	50.06±9.53	23.62–71.99
	width, μm	25.07±5.12	14.17–38.61	26.63±4.89	15.70–37.30
	height without cuticle, μm	15.83±3.48	8.23–22.73	18.15±3.14	13.13–25.20
Cells of the abaxial epiderma	**length, μm**	37.57±16.01	11.40–80.90	26.96±7.91	11.28–50.61
	width, μm	22.09±6.33	10.02–43.55	12.77±3.35	6.22–20.22
	height without cuticle, μm	13.01±3.93	5.00–21.15	7.48±1.51	5.44–11.92
The thickness of the cell wall of the epiderma with the cuticle, μm	**adaxial side**	9.60±1.71	5.65–13.96	6.48±1.58	4.32–9.60
	abaxial side	5.78±1.97	3.09–12.02	5.01±0.98	2.82–7.32
Palisade mesophyll	**width, μm**	73.85±10.03	54.49–96.01	62.30±8.68	36.07–72.94
Cells of the upper row of the columnar mesophyll	**length, μm**	60.37±7.42	44.14–75.84	41.61±5.99	30.77–54.05
	width, μm	8.11±1.68	4.45–12.73	8.37±1.71	4.40–13.56
Cells of the second row of columnar mesophyll	**length, μm**	26.18±3.31	19.53–33.84	19.85±3.92	10.95–28.00
	width, μm	8.67±1.32	6.53-12.12	10.16±1.49	6.43-12.58
Spongy mesophyll	thickness, μm	70.68±11.15	46.72-105.88	56.96±5.31	28.00-68.25
	length, μm	18.70±3.38	9.28–25.98	15.65±2.94	9.45–22.71
	width, μm	11.23±1.94	7.28–16.08	11.70±1.97	7.16–14.78
Intercellular space	length × width, μm	9.91×18.88		6.42×19.43	
Columnar/spongy		1.01		1.1	
Guard cells	length, μm	26.15±5.51	20.41–31.31	24.75±2.24	20.35–29.61
	width, μm	10.16±1.39	6.89–12.92	10.18±1.02	6.85–12.62
The total width of the stomata, μm		19.71±2.14	13.50–23.98	22.85±1.56	19.92–26.56
Density of stomata, pcs./mm^2		311,65±21.03	291–456	474.2±54.14	352–576
Number of epidermal cells	adaxial side, pcs./mm^2	1152,9±124.92	945–1376	1056.23±129.9	890–1305
	abaxial side, pcs./mm^2	1906.6±217.95	1648–2336	2557.4±384.57	1876–3040
Palisade coefficient		40.82		42.6	
Index of xeromorphism		22.1		30.3	
Density of trichomes of the abaxial epiderma, pcs./mm^2		94±16.33	32–114	14±1.63	10–37
Basal cells of uniseriate trichomes	length, μm	25.07±5.14	14.46–36.01	27.34±5.23	16.42–38.65
	width, μm	13.37±1.68	10.20–18.27	13.73±2.78	9.72–18.63
Stoma index, %		14.02		15.6	

Note. Mean values were calculated for 25–100 observations for each quantitative trait.

Based on known literature data an analysis of leaf trichomes of *Q. robur* and *Q. rubra* were conducted, the results are shown in table 2; and also our own research on the types of trichomes and their bases in mature leaves of *Q. robur* and *Q. rubra* was carried out (table 3).

Solitary trichomes were noted on the adaxial epiderma of mature leaves in *Q. robur* and *Q. rubra*; they occur very rarely; as non-glandular, single-celled, long, appressed. They are more characteristic of young leaves of both species, in mature ones they fall off, they can rarely occur mainly on the main vein; more often, the upper surface of the leaves of both species is bare (Hardin, 1976, 1979 a,b; Penas et al., 1994; Nikolic et al., 2003) (table 2, 3). For mature leaves, uniseriate trichomes were noted only in *Q. rubra* (fig. 1: B.1); appeared scattered; thick-walled with destroyed upper part, 1–2 basal cells often remained at the base. They belong to trichomes of the glandular type (Dyal, 1936). They were also noted for the upper epiderma of mainly young leaves of *Q. robur* (Penas et al., 1994; Fortini et al., 2009; Río et al., 2014) (table 2, 3). In addition to the considered solitary and uniseriate trichomes, for the adaxial epiderma of mainly young leaves of *Q. robur*, stellate trichomes are also indicated, and for *Q. rubra* – multiradiale, fasciculate, bulbous, rosulate (table 2).

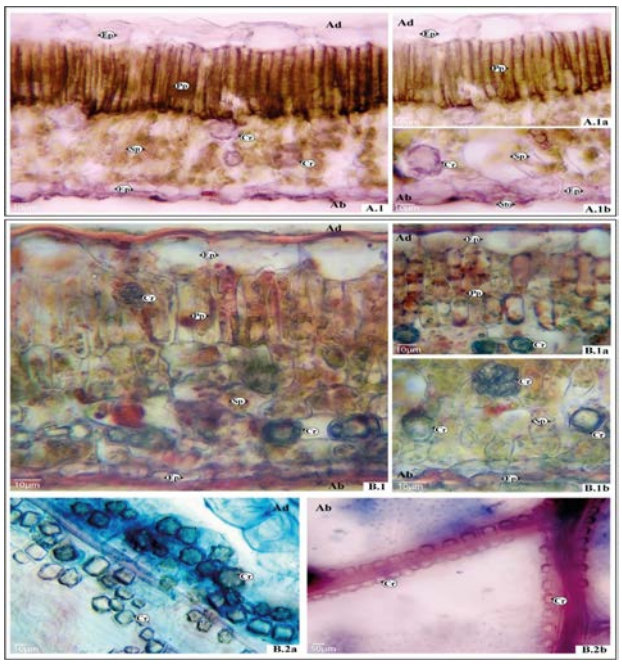

Fig 2. Anatomical structure of the leaf blade of: A. *Quercus robur* and B. *Quercus rubra*. 1. Cross sections of the leaf (a – adaxial side, b – abaxial side); 2. Frontal view of the leaf rib (a – adaxial side, b – abaxial side).Ad – adaxial side, Ab – abaxial side; Pp – palisade parenchyma; Sp – spongy parenchyma; Cr – calcium oxalate crystal; Sto – stomata

On the adaxial epiderma of mature leaves of *Q. rubra* and *Q. robur*, the bases of trichomes were found, among which several types can be distinguished, differing in the number and size of cells, the degree of cutinization of their walls. The bases of type I trichomes (fig. 1: A.2, B.1) have weakly cutinized intercalary walls (the base of the trichome was transparent or translucent when observed in SEM); anticlinal walls may not be thickened or cutinized (in the form of a rim from the edges of the base of the trichome); the cell walls of the epidermal cells adjacent to the base of the trichome can also be cutinized. The bases of trichomes of this type were radially surrounded by unmodified or modified (differing in smaller size and shape) epidermal cells. Type I bases correspond to unicellular bases of thin-walled trichomes (for example, uniseriate) according to Deng et al. (2014). The bases of type II trichomes (fig. 1: B.1) are characterized by markedly cutinized anticlinal and interclinal cell walls (the base is in the form of a dense, raised disc, does not shine through in SEM, is stained with Sudan III (Bačić & Miličić, 1985), safranin (Deng et al., 2014)); surrounded by smaller epidermal cells; correspond to single-cell bases of thick-walled trichomes (solitary, appressed laterally attached, simplified stellate, fasciculate) according to Deng et al. (2014). The bases of type III trichomes (fig. 1: B.2) were formed by collenchyma cells with crystalline inclusions; the base of the trichome was slightly above the epidermal cells (a pedestal structure) and due to cutinization had a darker color compared to the surrounding epidermal cells; corresponding to the multicellular bases of thick-walled trichomes (stellate, stipitate fasciculate, rosulate) (Deng et al., 2014).

In the adaxial epiderma of mature leaves of *Q. rubra*, the bases of trichomes were more abundant than in *Q. robur*; in both species, the bases of the trichomes were localized mainly along the veins and in their corners. In *Q. robur*, single-cell bases of trichomes of type I were rarely diagnosed; in *Q. rubra* trichome bases of all three types were present, but type II bases were more abundant (table 3).

Abaxial epiderma. The anticlinal walls of the epidermal cells of the abaxial leaf varied from straight, curved to slightly undulating in *Q. robur* and from undulating, sinuous, and deeply sinuous in *Q. rubra* (Figure 1: A.2, B.2). The epidermal cells of the upper and lower epiderma in *Q. robur* were similar in shape. The cells of the abaxial epiderma of *Q. rubra* were irregularly shaped. Epidermal cells of both species were prosenchymal along the veins. The length and width of epidermal cells were greater in *Q. robur* (37.57±16.01×22.09±6.33) than in *Q. rubra* (26.96±7.91×12.77±3.35); accordingly, the density of epidermal cells is lower in *Q. robur* (1906.63±217.95) compared to *Q. rubra* (2557.4±384.57) (table 1). On the abaxial side, around the veins in both species, a crystal-bearing cover was noticed (fig. 2: B.2b). Stomatal subsidiary cells were 5–6(7) in *Q. robur,* 5–7(8) – in *Q. rubra*; in *Q. robur* they did not differ from epidermal cells; in *Q. rubra* the anticlinal walls varied from straight to slightly wavy (fig. 1: A.2, B.2).

The stomata of both species were elliptical, raised above the surface of the epiderma, the size of the stomata in *Q. robur* – 26.15±5.51×19.71±2.14 μm (L×W) and in *Q. rubra* – 24.75±2.24×22.85±1.56 μm; stomata density in *Q. robur* was 311.65± 21.03/mm^2, in *Q. rubra* – 474.2±54.14/mm^2 (table 1). The average stomatal density of *Q. robur* determined in this study was 311.65±21.03 (varied from 291 to 456) (table 1); literary information about this indicator varies quite a lot (Mitrović et al., 1997; Uzunova et al., 1997; Sha Valli Khan et al., 1999; Kryvoruchko & Bessonova, 2018; Nikolic et al., 2003; Batos et al., 2010; Yücedağ et al., 2019), the smallest values are 133.7–148.5/mm^2 (Mitrović et al., 1997), the largest values are 530–791 (Nikolić et al., 2005) and 826/mm^2 (Yücedağ et al., 2019). The average density of *Q. rubra* stomata was 474.2±54.14 (varied from 352 to 576) (table 1), this indicator was slightly higher than that of *Q. robur*; accord-

Table 2

Leaf trichome types of *Quercus robur* and *Quercus rubra* (according to the literature)

Autors	Types of trichomes according to Deng et al. (2014)					
	ST, sST	F, sF	SOL	UN	CA	RO
Quercus robur						
Dyal, 1936			0/0			
Gellini et al., 1992; Bussotti & Grossoni, 1997				?/+	?/+	
Engel, 1993				-/+		
Penas et al., 1994			+'/+'	0/+		
Uzunova et al., 1997				+	+	
Bačlć, 1981; Bačić, Miličić, 1985;	?/+					
Fortini et al., 2009	+		+	+/+		
Nikolic et al., 2003, 2006			+'/+'	-/+		
Mehrnia et al., 2013	+/+	-/+	-/+			
Río et al., 2014				+/+		
Jankiewicz et al., 2017, 2021		+		?/+		
Quercus rubra						
Dyal, 1936			?/+	?/+		
Penas et al., 1994		+'/+	+'/+'	+'/+		+'/+'
Hardin, 1976, 1979 a,b	0, +'/+	0/+	0, +'/+	0, +'/+	0/+	
Kryvoruchko & Bessonova, 2017		+		+		

Note. Trichome types: ST –stellate; sST –simplified stellate; F – fasciculate: sF –stipitate fasciculate; SOL – solitary; UN – uniseriate; CA – capitate; RO – rosulate. Adaxial / abaxial epiderma: + – trichomes presented in both young and mature leaves; +' – trichomes presented in young leaves, in mature leaves they mostly fall off, occur occasionally; 0 – trichomes presented in young leaves and in mature leaves, they fall off completely; ? 0– no information; – – trichomes are absent.

ing to literature data (Phelps, 1976; Kramer & Kozlowski, 1979; Ashton & Berlyn, 1994; Yiotis et al. 2006; Gil et al., 2012; Fiorin, 2013; Kryvoruchko & Bessonova, 2017, 2018) varies from 281/mm^2 (Fiorin, 2013) to 583–695/mm^2 (Ashton & Berlyn, 1994). A higher stomatal index value in *Q. rubra* leaves compared to *Q. robur* is associated with a higher density of epidermal cells and stomata (table 1).

The most numerous trichomes of the lower epiderma of *Q. robur* and *Q. rubra* mature leaves are uniseriate, which are evenly distributed over the entire surface of the leaf blade and on the veins. Uniseriate trichomes in *Q. rubra* are mostly single, rarely combined into bundles of 2 trichomes; but often combined into bundles of 2 and really 3 in *Q. robur* trichomes (fig 1: A.2, B.2). The density of uniseriate trichomes was greater in *Q. robur*. Trichomes of this type in both species were 3–5-celled, thin-walled, with an enlarged basal cell; distal cells are smaller than basal cells. After weakening of the secretory function, the distal cells of uniseriate trichomes became smaller, deformed or broken off. The basal cell diameter was the same in both species (13.37±1.68 in *Q. robur*; 13.73±2.78 in *Q. rubra*) (table 1). Solitary trichomes are non-glandular, unicellular, and are characteristic mainly of the lower epidermis of *Q. robur* and *Q. rubra* young leaves (table 2); in mature leaves of both species occur very rarely, along the veins. In *Q. robur* the trichomes were straight; in *Q. rubra* – straight or wavy according to Hardin (1976).

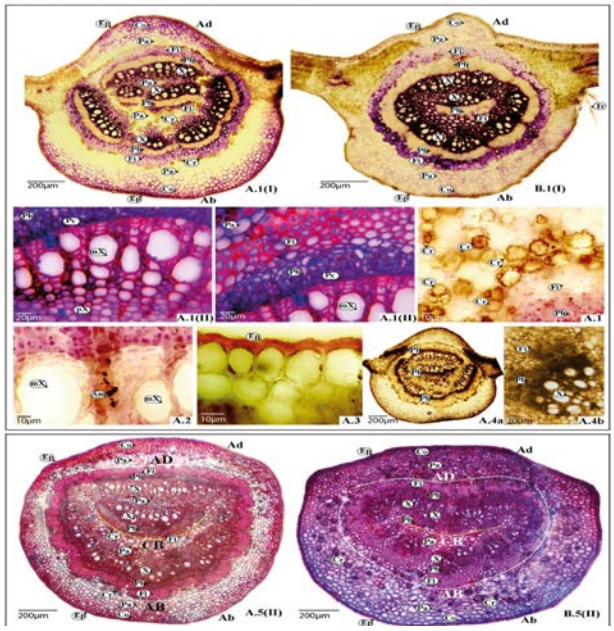

Fig. 3. Anatomical structure of the leaf midrib and petiole of: A. *Q. rubra*, B. *Quercus robur*. 1. midrib; 2. dark blue colour of amyloplasts in reaction with Lugol's solution; 3. orange-red coloration of the cuticle in reaction with Sudan III; 4. black coloring of phenolic compounds of the middle vein (a) and petiole (b) in the reaction with iron (III) chloride; 5. petiole in the medial part. I. Staining Phloroglucinol/HCl; II. Staining Safranin/Astra Blue. Ad – adaxial side, Ab – abaxial side; Ep – epiderma, Co – collenchyma, Pa – parenchyma, Fi – bundle-sheath of sclerenchyma fibres, Ph – phloem, X – xylem, mX – metaxylem; pX – protoxylem; Pc – procambium; Am – amyloplast; Tr – trichomes

Simplified stellate trichomes of *Q. robur* were located mainly along large veins and in their corners, occured much less often than uniseriate ones; consisted of 2–4(6) rays (3–4-cell hairs), which grew at the base at the same level; the shoulders of the rays were located parallel to the surface of the leaf; average shoulder length 110.99±28.04; base of type II trichomes (fig. 1: A.2). In mature leaves of *Q. rubra* along the midvein, near and in the axils of the lateral veins, stellate trichomes (multiradiale according to Hardin (1979b, fig. 32) very rarely occur (fig. 1: B.2). They differ from simplified stellate-trichomes by a larger number of rays (in *Q. rubra* – 6–8), which emerge from different levels (Hardin, 1976); trichome bases – type III (complex, according to Deng et al. (2014); in *Q. rubra* with a shoulder length of 134.78±14.64.

In mature leaves of *Q. rubra*, stipitate fasciculate trichomes occasionally occurred only in the axils of lateral veins that depart from the midvein. Trichomes of this type are thick-walled, with 6–8 rays; 289.24±42.44 long (fig. 1: B.2); trichome base – type III. In *Q. robur*, the researchers also found stipitate fasciculate trichomes (fig. 4.C; Jankiewicz et al., 2021). Capitate trichomes were very rare in the lower epiderma of mature leaves of *Q. robur*. These trichomes with a short, uniseriate stalk and a prominent, expanded unicellular head; belong to non-glandular trichomes (Hardin, 1976, 1979 a,b; Jones, 1986; Deng, 2014). In the literature, there were also references to these trichomes in the leaves of *Q. robur* (Gellini et al., 1992; Bussotti & Grossoni, 1997) and *Q. rubra* (Hardin, 1976, 1979 a,b); these trichomes were not detected in *Q. rubra*. Rosulate trichomes were given according to the literature mainly for young leaves of *Q. rubra*, which were located singly, mostly on the veins; these trichomes were very few in adult leaves (Penas et al., 1994). Rosulate trichomes are similar to stellate trichomes, but have thin-walled multicellular hairs that merge at the base; classified as glandular (Hardin, 1976) or intermediate types of trichomes (combining characteristics of glandular and non-glandular trichomes) (Jones, 1986). In the abaxial epiderma of adult leaves, trichomes of all three types were rarely observed in *Q. robur* and more often in *Q. rubra*, especially type III trichomes (table 3).

Table 3

Types of trichomes and their bases of mature leaves of *Quercus robur* and *Quercus rubra* (according to the results of current research)

Species	Trichomes						Types of trichome bases		
	sST	ST	sF	SOL	UN	CA	I	II	III
Adaxial epiderma									
Q. robur				+			+		
Q. rubra				+	++		+	+++	+
Abaxial epiderma									
Q. robur	++			+	+++	+	+	+	+
Q. rubra		+	+	+	+++		+	+	++

Note. Explanation of trichome types as in table. 2. + very rare, solitary trichomes; ++ scattered; +++ frequently

Anatomy of a cross section of a leaf blade. The material of this section was analyzed taking into account the information given in the literature regarding the anatomical structure of the cross-section of the leaf blade of *Q. robur* (Nikolić et al., 2005; Río et al., 2014; Martins et al., 2022) and *Q. rubra* (Abrams & Kubiske, 1990; Ashton & Berlyn, 1994; Río et al., 2014; Jankiewicz et al., 2017; Kryvoruchko & Bessonova, 2017, 2018). The leaf blade was thicker in *Q. robur* (180.64±10.29 μm), thinner in *Q. rubra* (136.11±6.12 μm) (table 1). On the adaxial and abaxial sides, the leaves of *Q. robur* and *Q. rubra* were covered with cuticle, which is thicker on both sides in *Q. robur* (table 1). The thickness of the cuticle of the studied species is slightly higher or varies within the parameters given by other authors (Ashton & Berlyn, 1994; Uzunova et al., 1997; Nikolić et al., 2005; Kryvoruchko & Bessonova, 2018). In the histochemical test with Sudan III, the cuticle acquired a pink color, indicating the presence of lipoids (cuticular wax). In a transverse section of each leaf, the adaxial and abaxial epiderma of both species consisted of a single layer of cells; adaxial epiderma with greater cell thickness than abaxial. The thickness of cells of the adaxial epiderma was greater in *Q. rubra* (18.15±3.14 μm) than in *Q. robur* (15.83±3.48 μm); the thickness of cells of the abaxial epiderma, on the contrary, was greater in *Q. robur* (13.01±3.93 μm) compared to *Q. rubra* (7.48±1.51 μm). Calcium oxalate crystals were found mainly in the cells of the upper epiderma.

Leaves of *Q. robur* and *Q. rubra* with mesophyll clearly differentiated into palisade and spongy (fig. 2: A.1, B.1). Palisade parenchyma with one or two layers of cells in both species. In the two-layered palisade parenchyma of both species, the layer adjacent to the adaxial epidermis had densely arranged prosenchymal cells, without noticeable air intercellular spaces; cells of the next layer were shorter and with more intercellular spaces.

The palisade mesophyll was located under the adaxial epiderma and thicker in *Q. robur* (73.85±10.03 μm) than in *Q. rubra* (62.30±8.68 μm). The cells adjacent to the epidermal cells were oblong; the ratio of length to width was greater in the cells of the palisade mesophyll in the leaves of *Q. robur* (the elongation factor reaches 5.95–8.07 in *Q. robur* and 4.15–6.9 in *Q. rubra*), they were densely arranged, there was almost no space

between them. The cells of the inner layer of the palisade mesophyll were shorter (the elongation factor reached 2.9–2.79 in *Q. robur* and 1.7–2.22 in *Q. rubra*), and are more loosely arranged. According to histochemical reactions with iron (III) chloride, phenolic compounds were detected mainly in the palisade mesophyll; reaction with Lugol's solution revealed the presence of starch grains in palisade and spongy mesophyll cells. The spongy mesophyll of the *Q. robur* and *Q. rubra* leaves was formed by loosely placed rounded or isodiametric, cylindrical or irregularly shaped cells, the sizes of which were slightly larger in *Q. robur* (Table 1), arranged in 3–4 layers, with pronounced intercellular spaces; the cell elongation factor in *Q. robur* was 1.27–1.67 and in *Q. rubra* – 1.31–1.53. Druses and prismatic crystals in the spongy mesophyll of *Q. rubra* leaves were more abundant than in *Q. robur* (fig.2: A.1, B.1). The ratio of the thickness of the palisade and spongy mesophyll in the *Q. robur* and *Q. rubra* leaves was about 1:1. The palisade ratio of *Q. robur* leaves was 40.82%; *Q. rubra* – 42.6%. The difference between the species may appear mainly as a result of a thicker layer of palisade parenchyma due to an additional second layer of cells (Shahbaz et al., 2015).

Anatomy of the middle vein. On the cross-section of the leaf, the midvein of *Q. robur* and *Q. rubra* were rounded in outline; more convex on the abaxial side, conical on the adaxial side (fig. 3: A.1, B.1); average indicators (H×W) were slightly higher in *Q. rubra* (1112.22×1059.49) (table 4). The middle veins of the leaves were covered with one layer of epiderma with small cubic-oval cells, with a developed cuticle, containing crystalline inclusions. Epidermal cells had larger average values of width in *Q. rubra* (13.39±4.94), and somewhat larger values of height in *Q. robur* (8.42±1.78) (table 4). In *Q. robur*, stellate trichomes were often visible on the abaxial side in the corners between the vein and the leaf blade (fig. 3: B.1); in *Q. rubra*, complex stellate and fasciculate trichomes rarely occured.

The central conducting bundle was surrounded by a shealth consisting of collenchyma and parenchyma of the primary cortex (fig. 3: A.1, B.1). In both species, the collenchyma was located under the epiderma, on the adaxial side with 3–4 layers of cells, on the abaxial side – 4–8; in shape, the cells were round, oval, square or irregular in shape; larger on the abaxial side. Calcium oxalate crystals occur in collenchyma cells. The thickness of the collenchyma on both sides was greater in *Q. rubra*, but the diameter of the cells and the thickness of their walls were greater in *Q. robur*. Both species had 5–8 layers of storage parenchyma under the collenchyma; cells were devoid of chloroplasts, mostly round in shape; cell sizes were larger on the abaxial side, and somewhat larger in *Q. rubra* (table 4).

The total thickness of the primary cortex layer was larger on the abaxial side and reached a higher average value in *Q. rubra* (217.32±42.36), compared to *Q. robur* (135.50±40.43). Calcium oxalate crystals were scattered throughout the parenchyma of the primary cortex, but the largest number of them was localized in the cells of the inner layers of the parenchymal lining, which were adjacent to the sclerenchyma. Crystals are large, occupy most of the cell, mostly in the form of druses, prismatic crystals are rare (mainly in *Q. rubra*) (fig. 3: A.1). The parenchyma of *Q. rubra* is characterized by a greater number of crystalline inclusions. The vascular system of the middle vein was surrounded by a dense ring of sclerenchyma (pericyclic fibers), which separatds the parenchyma of the primary cortex from the phloem (fig. 3: A.1, B.1). The thickness of the ring of the sclerenchyma coverage was greater in *Q. rubra* (67.77±16.58), its thickness is often the same on both sides; in *Q. robur*, the sclerenchyma lining was thinner (46.79±21.36) and usually more developed on the adaxial side; fibers were arranged in 3–8 rows, their diameter and cell wall thickness did not differ significantly in both species. The sclerenchyma ring was almost straight on the adaxial side; distinctly convex on the abaxial side. Crystalline inclusions occasionally appear in the sclerenchyma of both species.

There are three blocks in the structure of the vascular system (fig. 3: A.1, B.1). Adaxial and abaxial blocks consist of primary conducting tissues; the central one – from the secondary ones. The adaxial vascular block is convex, consists of phloem layers (adjacent to the sclerenchyma ring), and in the middle is the procambium, then the primary xylem, which has differentiated metaxylem and protoxylem (fig.3: A.1). The central and abaxial blocks of conducting tissues consist of protoxylem, differentiated metaxylem, cambial/procambial cells, and phloem. The abaxial block of conducting tissues is arched and separated from the central block by 5–8 layers of storage parenchyma with crystalline inclusions. Between the adaxial and central blocks of conductive tissues in *Q. rubra* there are 3–5 layers of storage parenchyma; in *Q. robur*, the xylems of the central and adaxial sides are in contact.

The average thickness of the phloem layers of *Q. robur* (50.16±14.56) and *Q. rubra* (50.89±9.18) did not differ significantly; also, the phloem thickness of both species was almost the same in the adaxial and abaxial vascular blocks and somewhat thinner in the central one. The average xylem thickness in *Q. rubra* (124.21±27.24) was greater than in *Q. robur* (88.55±18.61); the average vessel diameter is also somewhat larger in *Q. rubra* (29.89±6.32), compared to *Q. robur* (23.06±6.25). In terms of size, the paren-

Table 4

Anatomometric indicators of the *Quercus robur* and *Quercus rubra* middle vein and medial part of petiole

Parameters		Middle vein		Petiole	
		Q. robur	***Q. rubra***	***Q. robur***	***Q. rubra***
Diameter of cross sections	height, μm	849.19±44.38 765.02–1137.1	1112.22±82.07 955.99–1483.84	1143.02±195.39 874.72–2187.93	1392.07±155.61 1056.21–1855.32
	width, μm	863.18±59.10 781.36–1210.4	1059.49±98.17 968.17–1384.57	1238.28±148.87 713.82–1898.15	1281.17±115.28 997.89–1757.70
Epidermal cells	width, μm	8.97±2.21 2.22–15.22	13.39±4.94 7.54–21.75	11.08±2.18 8.57–19.05	14.68±3.80 8.52–23.74
	height without cuticle, μm	8.42±1.78 5.89–11.55	5.81–1.01 4.50–7.33	10.88±1.58 8.48–14.34	8.63±1.97 5.92–13.27
The thickness of the outer cell wall of the epiderma with the cuticle, μm		8.25±1.19 4.82–11.37	6.00±1.51 4.29–9.43	8.52±2.04 4.62–11.62	7.85±1.78 4.05–10.97
The thickness of the primary cortex layer, μm	from the adaxial side	117.36±23.77 69.04–212.74	165.54±26.77 81.29–249.25	174.20±51.15 106.89–310.97	173.97±39.37 88.87–278.74
	from the abaxial side	135.50±40.43 82.39–235.83	217.32±42.36 118.68–297.66	198.21±76.73 172.64–341.98	204.47±40.40 114.73–313.02
The thickness of the cortex collenchyma layer, μm	**from the adaxial side**	44.90±8.73 29.37–60.53	68.17±19.58 36.01–103.36	100.51±31.89 81.28–178.73	74.23±19.68 46.01–113.96
	from the abaxial side	37.34±9.86 24.38–52.22	48.07±10.56 31.05–77.50	97.90±19.92 72.47–170.80	50.07±10.56 31.05–79.50
Collenchyma cell wall thickness, μm		3.43±0.85 1.52–5.68	2.05±0.49 1.29–2.78	3,5±0.42 2.16–6.48	3.06±0.74 1.61–4.26
Diameter of collenchyma cells, μm	from the adaxial side	18.41±6.31 8.09–29.98	11.46±2.729 7.29–16.32	20.95±7.47 9.80–37.17	13.94±2.90 9.29–20.63
	from the abaxial side	19.37±6.40 7.76-34.65	17.88±4.44 9.03-26.47	26.82±7.09 13.47-45.16	22.53±5.00 12.81-32.88
Diameter of parenchyma cells, μm	**from the adaxial side**	15.29±5.93 8.49–17.26	17.44±3.69 8.87–28.81	16.27±2.17 6.18–18.57	16.28±3.54 7.32–29.47
	from the abaxial side	25.27±7.88 10.10–46.57	38.50±8.63 11.63–81.19	30.95–9.53 12.83–61.69	31.51±9.40 10.44–65.48
The thickness of the sclerenchyma shealth, μm		46.79±21.36 30.14–102.67	67.77±16.58 30.17–119.27	56.52±23.11 32.39–112.97	98.97±19.94 39.30–122.03
Diameter of sclerenchymal fibers, μm		13.87±5.02 3.74–26.53	13.26±±4.56 5.75–27.52	16.80±5.23 7.13–36.90	16.50±7.60 3.70–38.97
The thickness of the walls of sclerenchyma shealth, μm		2.11±0.49 0.85–3.22	2.81±0.80 0.88–4.19	3.57±0.57 1.71–5.74	3.58±0.79 1.84–6.55
Phloem thickness, μm		50.16±14.56 30.76-84.65	50.89±9.18 32.23–78.47	61.96±14.71 30.46–91.40	60.07±19.42 24.56–107.86
Xylem thickness, μm		88.55±18.61 53.76–109.19	124.21±27.24 74.52–204.45	124.38±28.02 71.11–201.42	126.09±30.24 75.21–205.15
Vessel diameter, μm		23.06±6.25 10.77–35.00	29.89±6.32 10.21–50.10	24.55±6.58 7.54–36.22	31.72±7.61 17.55–56.23
Diameter of core parenchymal cells, μm		15.83±5.74 4.59–31.37	19.49±9.43 7.12–39.50	17.27±6.44 5.10–45.89	20.12±7.79 8.79–46.78
Diameter of crystals in the parenchyma of the primary cortex, μm		18.78±6.09 8.57–32.00	23.71±8.78 10.79–44.27	26.48±7.97 9.49–45.94	28.58±8.11 10.11–46.63
Diameter of crystals in the pith, μm		14.68±3.80 8.37–21.01	17.08±6.73 5.69–33.50	15.33±3.24 10.38–27.37	17.28±4.14 7.77–36.83

Note. Mean values were calculated for 25–100 observations for each quantitative trait

chymal cells of the pith and their crystalline inclusions were somewhat larger in *Q. rubra* (table 4).

After the histochemical reaction with phloroglucin/HCl, collenchyma of the primary cortex, sclerenchyma and xylem acquired a crimson-red color, indicating their lignification (fig 3: A.1(I), B.1(I)). Histochemical reaction with Sudan III gave an orange-red color of the cuticle of the epiderma (presence of cuticular wax) (fig. 3: A.3). Using Lugol's solution, amyloplasts were detected in the parenchyma of the primary cortex and the conducting system (Figure 3: A.2). The reaction with iron (III) chloride showed the high-

est concentration of phenolic compounds in the middle vein in the phloem parenchyma (fig. 3: A.4a).

Petiolar anatomy. In a cross-section, the medial (middle) part of the *Q. rubra* petioles was rounded, convex on the adaxial and abaxial sides, without ribs; petiole of *Q. robur* is rounded in outline and slightly compressed from adaxial to abaxial sides; on the adaxial side, straight or slightly convex, also here the ribs became visible in the view of small rounded-triangular protrusions; from the abaxial side, the petiole was rounded (fig. 3: A.5, B.5). The average values of petiole height were slightly larger than width (1392.07×1281.17) in *Q. rubra*; and on the contrary, petioles were larger in width (1143.02×1238.28) in *Q. robur* (table 4; fig. 3: A.5, B.5). The epiderma of petioles is single-layered, consists of cubic-oval cells and was covered with a thick cuticle. The average values of epidermal cell width were greater in *Q. rubra* (14.68±3.80), and they were greater in height in *Q. robur* (10.88±1.58) (table 4). Solitary and fasciculate trichomes were observed on petioles of both species, mainly on the adaxial side in the upper surface groove.

The primary cortex was under the epiderma, its thickness was almost the same in the two species; it was more developed on the abaxial side. The outer layer of the bark was represented by collenchyma, mainly with round-oval or square cells. Collenchyma may include 5 to 12 rows of cells in *Q. rubra* and 4 to 8 rows in *Q. robur*; it reaches its greatest thickness in the ribs, on the abaxial and adaxial sides. In the petioles of *Q. robur*, especially on the adaxial side, the thickness of the collenchyma layer, the size of the cells, and the thickness of their membranes are greater than those of *Q. rubra*. The parenchyma of the primary cortex is located between the collenchyma and the mechanical shealth of the vascular system, had more cell layers in *Q. rubra* – 8–15 than in *Q. robur* – 6–12. Cells of rounded, oval or irregular shape, in size in both species are almost the same; the largest cells were concentrated on the abaxial side near the shealth of the mechanical tissue. Scattered calcium oxalate crystals were visualized in the tissues of the primary cortex, they reach the highest concentration in the inner layers of the parenchyma around the ring of the mechanical shealth of the conducting system, and are also accumulated in the parenchyma on the adaxial side (Fig. 3: A.5, B.5). A significant number of crystalline inclusions were present in petiole sections of both species; their average diameter was larger in *Q. rubra* (28.58±8.11) than in *Q. robur* (26.48±7.97) (table 4).

The structure of the vascular system of petioles in the medial part of *Q. rubra* differed in the complete fusion of vascular bundles in the adaxial and abaxial blocks and complete or partial fusion in the central blocks; in *Q. robur* bundles the adaxial and abaxial blocks merged completely or partially, the central block of secondary vascular bundles was visualized (fig. 3: A.5, B.5). The xylem of the central block of the vascular bundles of *Q.rubra* was clearly separated by parenchymal tissue from the xylem of the adaxial block, the vascular bundles of the central and adaxial blocks were in contact in *Q. robur* (fig. 3: A.5, B.5). The shealth of sclerenchymal fibers around vascular system was thicker in *Q. rubra* – 98.97±19.94 (in *Q. robur* (56.52±23.11) (table 4). The shealth consists of 6–10 dense layers of sclerenchyma fibers, which in cross-section are round, oval, triangular, rhombic or irregular in shape. The diameter and thickness of the cell wall of fibers of both types were almost the same. The average values of the phloem layer thickness did not differ significantly in *Q. rubra* (60.07±19.42) and *Q. robur* (61.96±14.71). Phloem elements are with thin walls; in shape from rounded, oval, triangular, rhombic to irregular. The average thickness of the xylem in *Q. rubra* (126.09±30.24) was slightly greater than in *Q. robur* (124.38±28.02); the average vessel diameter was also larger in *Q. rubra* (31.72±7.61), compared to *Q. robur* (24.55±6.58) (table 4). The average values of the diameters of the pith parenchymal cells were slightly larger in *Q. rubra* (20.12±7.79), and they also contained larger crystalline inclusions (17.28±4.14) (Table 4).

In the histochemical reaction with phloroglucin/HCl, collenchyma of the primary cortex, sclerenchyma, and xylem acquired crimson-red color in all cross-sections of petioles of both species, indicating their lignification. Cuticles of the epiderma in all cross-sections of petioles of both species acquired an orange-red color (cuticular wax) in the histochemical reaction with Sudan III. According to the histochemical reaction with iron (III) chloride, the highest concentration of phenolic compounds was identified in the xylem and phloem parenchyma of the petiole (fig. 3: A.4b). Amyloplasts were detected by reaction with Lugol's solution in the parenchyma of the primary cortex, especially in the inner layers adjacent to the shealth of mechanical tissues, cells of the parenchyma of the pith and pith rays.

The leaves of *Q. rubra* and *Q. robur* are a promising object for pharmacognostic study and introduction into official medicine. In this study, it was important to identify the qualitative and quantitative variability of the anatomical features of the leaf blade structure of *Q. rubra* in comparison with *Q. robur* and to evaluate the possibility of their use for determination of the identity, standardization and quality control of medicinal plant raw materials. Anatomical features of the structure of leaves, such as: type of pubescence, contour of the cell wall of the epiderma, shape and density of stomata, structure of secondary cells, presence

of adaxial collenchyma, etc. are the most informative for identification of taxa (Zhou et al., 1995).

The epidermal cells of the adaxial surface of the leaves of both species had a similar shape of quadrangles or polygons with straight or curved anticlinal walls. The cells of the abaxial epidermis of *Q. rubra* varied in the character of the anticlinal walls from straight, curved to weakly undulating in Q. robur and from undulating, sinuous, and deeply sinuous in *Q. rubra*. The sizes of adaxial epidermal cells were slightly larger in *Q. rubra*, which correlates with their lower density. Abaxial epidermal cells awee larger and less dense in *Q. robur*. The abaxial epidermal layer was thicker in *Q. robur*; the adaxial – thicker in *Q. rubra*. The cuticular layer was more developed in *Q. robur* leaves; on the adaxial side of the leaves of both species, the cuticle was somewhat thicker. The thickness of the cuticle of *Quercus* species varies depending on the habitat conditions, in particular, it decreases under conditions of lack of light (Bahamonde et al., 2018; Kryvoruchko & Bessonova, 2018), or increases in leaves collected from trees of polluted habitats (Kryvoruchko & Bessonova, 2017).

A general pattern of pubescence in mature leaves of *Q. robur* and *Q. rubra*, as in other *Quercus* species (Hardin, 1979a), is a greater density of it and a greater variety of trichomes on the abaxial side compared to the adaxial side. Trichomes are important for species identification in genus *Quercus*; particular types of trichomes are characteristic of subgenera and sections. *Q. robur* is a representative of section *Quercus* (= subg. Lepidobalanus, white oaks) for which species the stellate trichomes are diagnostic (Hardin, 1979a; Jones, 1986); the presence of simplified stellate trichomes according to Deng et al. (2014) on the adaxial side in mature leaves was confirmed by the results of this study in *Q. robur*. For section Lobatae (= subg. Erythrobalanus, red oaks), to which *Q. rubra* belongs, the appressed laterally attached unicellular, multiradiate and rosulate trichomes (Hardin, 1979a; Jones, 1986) are diagnostic. Among the mentioned types of trichomes based on literature data and mostly for young leaves of *Q. rubra*, multiradiate (Hardin, 1976, 1979 a,b) and rosette rosulate (Penas et al., 1994) trichomes are cited. In this study, only multiradiate (stellate according to Deng et al. (2014) trichomes very rarely along the midvein and in the axils of the lateral veins were observed in mature leaves of *Q. rubra*. Common to mature leaves of both species are solitary trichomes, rarely found on both sides of the leaf blade; trichomes of this type are common in species of the genus *Quercus* (Kim et al., 1992).

Also, in the mature leaves of *Q. robur* and *Q. rubra*, on the abaxial side, among the preserved trichomes, uniseriate glandular ones were identified, which absolutely prevail among the trichomes of other types. Trichomes of this type are the most basic glandular trichomes of Fagaceae Dumort. representatives and are typical in all sections of the genus *Quercus* (Jones, 1986), they are of the same type in structure, therefore the use of features of their structure in systematics is not appropriate, unlike non-glandular trichomes, which are characterized by a significant diversity of structure (Thomson, Mohlenbrock, 1979; Hardin, 1979a,b; Jones, 1986; Valencia, Delgado, 2003; Río et al., 2014). Examination of uniseriate trichomes of *Q. robur* under SEM showed that the basal cell is densely covered with plates of epicuticular wax (Engel, 1993, fig. 1; Jankiewicz et al., 2017, fig. 1d). The essential oil is capable of dissolving epicuticular wax crystalloids after release from glandular trichomes (Engel, 1993). Because of the thick walls and layering of wax, the basal cells of uniseriate trichomes are well preserved even in old leaves of *Q. rubra* and *Q. robur*. Both species also have stipitate fasciculate trichomes (Jankiewicz et al., 2021; Penas et al., 1994; Kryvoruchko & Bessonova, 2017; Hardin, 1976, 1979 a,b), which we occasionally noted in mature leaves of *Q. rubra* in the axils of the lateral veins, and they were also found on petioles of both species; capitate trichomes (Gellini et al., 1992; Bussotti & Grossoni, 1997; Uzunova et al., 1997; Hardin, 1976, 1979 a,b) were rarely noted by us only for *Q. robur.* Stipitate fasciculate, solitary and capitate trichomes are particularly unstable, so the identification of certain types of trichome bases indicates their existence in young leaves (Hardin, 1976; Jones, 1986; Kim et al., 1992; Buck & Bidlack, 1998; Panahi, 2012; Deng et al., 2014). The bases of trichomes of I–III types were found on both sides of leaf blade in *Q. rubra*. The rather high density of the bases of *Q. rubra* trichomes indicates little persistence of the trichomes, most of which fall off when the leaf matures. Trichomes of *Q. robur* were more resistant to falling; trichome bases were rare in this species.

Thus, reliable diagnostic features of mature leaves pubescence of *Q. robur*, by which they can be distinguished from leaves of *Q. rubra*, are scattered simplified stellate trichomes mainly on the adaxial side of the leaf; solitary and capitate trichomes are very rare; mature leaves of *Q. rubra* are characterized by a lower density of uniseriate trichomes, the presence of trichome bases of I–III types on both sides of the leaf; fasciculate and stellate trichomes are also rarely found. As other *Quercus* species, the studied two spe-

cies have dorsoventral and hypostomatous leaves with anomocytic stomata that are slightly raised above the epidermal surface (Río et al., 2014).

For the ultrastructure of the *Q. robur* stomata, which was studied in detail under SEM, it was determinated that the outer walls of the guard cells are surrounded by thickening of the outer wall guard cells, which, like the entire leaf epiderma, are covered with continuous wax layer, on which numerous crystalloids of epicuticular wax in the form of fringed plates are superimposed (Bacic, 1981, fig. 2; Prasad & Gülz, 1990, fig. 1, A-D; Engel, 1993, fig. 1; Russotti & Grossoni, 1997 , Uzunova et al., 1997, fig. 2; fig. 3; Fortini et al., 2009, fig. 3,a; Río et al., 2014, fig. 2,j; Jankiewicz et al., 2017, fig. 1). Stomata of *Q. rubra* were also examined under a SEM in connection with the study of the model of water loss in expanding leaves (Turner & Heichel, 1977, fig. 5; Kane et al., 2020, fig. 5,7); visually, they differ from the stomata of *Q. robur* by less development of epicuticular wax plates.

The stomata of both species are almost the same size. The abaxial epidermis of *Q. rubra* leaves is characterized by a greater density of stomata. Average stomatal densities of *Q. robur* and *Q. rubra* are in the range established for other plant species growing in arid habitats (133–537/mm2, according to Yiotis et al., 2006; Gil et al., 2012). The stomatal density values of *Q. robur* and *Q. rubra* determined in this study were within the limits of the indicators indicated in the literature; the ranges of stomatal density variation in both species overlapped. Various environmental factors (e.g., water availability, light intensity, photoperiod) can influence epidermal cell stretch and thus affect stomatal density (Hoof et al., 2005). That is probably why, when identifing the dependence of *Quercus* stomata density on leaf illumination, the results of different researchers may be contradictory (Abrams &Kubiske, 1990; Batos et al., 2010). For example, an increase in stomatal density in *Q. robur* and *Q. rubra* was shown when growing under better lighting conditions (Abrams & Kubiske, 1990; Kryvoruchko & Bessonova, 2018); according to other data, this indicator increases in *Q. robur* and other species under conditions of shadow growth (Bruschi et al., 2003; Batos et al., 2010); or under different light conditions, populations of *Q. rubra* trees did not differ statistically significantly for traits of stomatal density or stomatal index (Daly & Gastaldo, 2010).

The structure of the cross-sections of the *Q. robur* and *Q. rubra* leaves is of the same type, the differences were indicated in the greater length and at the same time in the smaller width of the cells of the palisade parenchyma in the leaves of *Q. robur*. The palisade parenchyma of *Q. robur* and *Q. rubra* can have from one to two, rarely three layers of cells, depending on the conditions of growth, in particular, lighting or pollution of the environment (Ashton & Berlyn, 1994; Nagel et al., 1998; Río et al., 2014; Kryvoruchko & Bessonova, 2017). Increasing the layers of the palisade parenchyma to two or three provides better photosynthetic light utilization efficiency, especially in species in which trichomes or a wax layer reduce radiation absorption (Rotondi et al., 2003).

In both species, the thickness of the columnar parenchyma was almost the same as the thickness of the spongy parenchyma (the ratio is approximately 1:1). This ratio of columnar and spongy mesophyll thickness was also noted for other species of the oak genus (Shahbaz et al., 2015). The palisade coefficient, which characterizes resistance to drought and the degree of xeromorphism of the structure (Kryvoruchko & Bessonova, 2017), in the leaves of the studied species was approximately the same and laid within 40 to 50%, which corresponds to its average value.

Drusen and prismatic crystals are more abundant in the spongy mesophyll of *Q. rubra* leaves. Compared to other oak species, crystalline inclusions in the spongy mesophyll of *Q. robur* leaves occur less often (Río et al., 2014), and are mainly represented by druses. The presence of starch and tannins was confirmed in the mesophyll (mainly palisade) of leaves of both species. Ergastic substances in plant tissues, mainly tannins and calcium oxalates, play an important role in the control of cellular ion and osmotic balance, which is crucial in the adaptive resistance of plants to water stress (Franceschi & Horner, 1980; Rotondi et al., 2003). Crystalline inclusions of calcium salts ensure the balance of cellular ions (sodium and/or potassium), protection of plants from being eaten by animals, stiffness and support functions of tissues, detoxification of oxalic acid or aluminum and/or heavy metals, absorption and reflection of light, etc. (Franceschi & Horner, 1980; Franceschi & Nakata, 2005; He et al., 2012). The presence or absence of crystals, their type and their chemical composition can be used as taxonomic features (Meric, 2009).

Phenolic compounds are secondary metabolites responsible for adaptation and resistance to aggressive environmental factors. They participate not only in plant defense mechanisms against fungal pathogens, but also against herbivorous insects (Lattanzio et al., 2006, 2009). The cuticular layer, as well as phenolic compounds that are concentrated in vacuoles, in the walls of epidermal cells, especially in the mesophyll of the plant, perform the function of absorbing UV radiation and prevent photodamage of the more sensitive tissues of the mesophyll inside the leaf (Day et al., 1993; Rotondi et al., 2003).

The average leaf blade thickness determined in this study was slightly larger in *Q. robur*. The values of the thickness of the leaves of both species overlap, which is also shown in the literature (Abrams & Kubiske, 1990; Valladares et al., 2002; Río et al., 2014; Sevillano et al., 2016). The thickness of the leaf blade can be an indicator of the light use strategy of plants (Sevillano et al., 2016). The thickness of leaves in individuals of the same species decreases with increasing shading, which has been experimentally confirmed, in particular for *Q. robur* (Valladares et al., 2002; Sevillano et al., 2016) and *Q. rubra* (Abrams & Kubiske, 1990).

The midribs of *Q. rubra* and *Q. robur* have the same anatomical structure, which is similar to other oak species (Río et al., 2014; Shahbaz et al., 2015). The middle vein is covered with a single-layered epiderma with a pronounced cuticle layer; the primary cortex contains collenchyma and more developed storage parenchyma, the vascular system is surrounded by a dense ring of mechanical tissues; the vascular system consists of primary vascular tissues that are localized in the peripheral adaxial and abaxial blocks (bundles), and secondary ones that form the central block (bundle). The differences in the anatomical structure of *Q. rubra* from *Q. robur* were the greater development of parenchyma and collenchyma of the primary cortex, sclerenchyma shealth; a larger number of secondary conducting bundles in the central unit; the presence of the pith parenchyma between the xylems of the central and adaxial blocks; a greater number of crystalline inclusions in the primary cortex and parenchyma of the vascular bundle. Amyloplasts were found in the parenchyma of the primary cortex and the vascular system. Phenolic compounds in the midrib in both species were concentrated mainly in the phloem.

Features of the petiole anatomical structure in plants, in particular species of the genus *Quercus*, have species uniqueness, therefore they are widely used as diagnostic feature in determining species affiliation (González-Rodríguez & Oyama, 2005; Río et al., 2014; Shahbaz et al., 2015; Fortini et al., 2015). In pharmacognostic studies, the analysis of the features of petiolar anatomy becomes a convenient tool for determining the identity of species and standardization of medicinal plant raw materials. According to the results of the study of anatomical sections of petioles of *Q. rubra* and *Q. robur* in the medial part, diagnostically significant features that can be used for species identification were identified.

Conclusions

The main differences in the cross-sections of the medial part of the *Q. rubra* petioles were the complete fusion of the vascular bundles in the adaxial and abaxial blocks; by a clear separation of the well-developed xylem of the central block from the xylem of the adaxial block by the pith parenchyma. Also, the cross-sections of the medial part of the *Q. rubra* petioles differed in their rounded shape, the absence of lateral ribs on the adaxial side, and the uniform thickness of the layer of the primary cortex on all sides of the petiole; the average dimensions of cross-sections reached greater values, and the associated dimensions of sclerenchyma, xylem, cortex and pith parenchyma were larger. The anatomical structure of the medial section of the *Q. rubra* petiole of is similar to the structure of the middle vein; in *Q. robur* it differed by partial fusion of bundles in adaxial and abaxial blocks and isolation of bundles in the central block of vascular tissues. Petioles of both species, in contrast to the middle veins, had larger diameters, did not have a conical projection of the primary cortex on the adaxial side; had a greater thickness of the mechanical tissues of collenchyma and sclerenchyma, as well as a greater number and larger sizes of crystalline inclusions; dimensional indicators of vascular tissues did not differ significantly between species and in different parts of anatomical sections of petioles and midrib. In the epiderma of petioles of both species, solitary and fasciculate trichomes were noted; in contrast to the midvein, which, in addition to fasciculate trichomes, included simplified stellate (in *Q. robur*) and stellate (*Q. rubra*) trichomes. According to histochemical reactions, the presence of wax-like substances, lignified tissues, tannins and starch in petioles of both species was confirmed. If in the middle vein tannins were mainly concentrated in the phloem, then in the petioles the largest number of them would be noted in the parenchyma of the vascular bundles. For comparison, in the cork of *Q. robur*, polyphenols are mainly accumulated in the cell walls of the tracheas, as well as in the cells of the ray parenchyma (Masson et al., 1994; Likhanov et al., 2019).

Therefore, the results of the research made it possible to identify the anatomical characteristics of the leaf blade and petiole of *Q. rubra* and *Q. robur*, which have diagnostic value and can be used to identify medicinal raw materials of these species. It is shown that the following are of the greatest diagnostic significance: the nature of pubescence of leaves, midribs and petioles, quantitative indicators and the nature of the distribution of crystalline inclusions in different parts of leaves, features of the structure of the vascular system of the midrib and petiole. Most of the dimensional indicators of the anatomical structure of the leaf plate varied in both species and cannot be used as reliable in the identification of raw materials.

BIBLIOGRAPHY

Abrams M.D., Kubiske M.E. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: Influene of light regime and shade-tolerance rank. *Forest Ecology and Management,* 1990. 31(4), 245–253. doi:10.1016/0378-1127(90)90072-J

Ashton P.M.S., Berlyn G.P. A comparison of leaf physiology and anatomy of *Quercus* (section *Erythrobalanus* – Fagaceae) species in different light environments *American Journal of Botany,* 1994. 81(5), 589–597. doi:10.2307/2445734

Bačić T., Miličić D. Contribution to the leaf anatomy of *Quercus Ilex* L. *Acta Botanica Croatica,* 1985, 44, 23–31.

Bačić T. Investigations of stomata of three oak species with light and scanning electron microscope. *Acta Botánica Croatia,* 1981. 40, 85–90.

Bahamonde H.A., Gil L., Fernández V. Surface. Properties and permeability to calcium chloride of *Fagus sylvatica* and *Quercus petraea* leaves of different canopy heights. *Frontiers in Plant Science,* 2018, 9, 494. doi: 10.3389/fpls.2018.00494

Barthlott W., Neinhuis C., Cutler D., Ditsch F., Meusel I., Theisen I., Wilhelmi H. Classification and Terminology of Plant Epicuticular Waxes. *Botanical Journal of the Linnean Society,* 1998, 126(3), 237–260. doi: 10.1111/j.1095-8339.1998.tb02529.x

Batos B., Vilotic D., Orlovic S., Miljkovic D. Inter and intra-population variation of leaf stomatal traits of *Quercus robur* L. in Northern Serbia. *Archives of Biological Sciences,* 2010, 62(4), 1125–1136. doi:10.2298/ABS1004125B

Berlyn G.P., Miksche J.P. Botanical Microtechnique and Cytochemistry. *Ames: Iowa State University Press,* 1976, 1256–1231.

Boratynski A., Marcysiak K., Lewandowska A., Jasinska A., Iszkulo G., Burczyk J. Differences in leaf morphology between *Quercus petraea* and *Q. robur* adult and young individuals. *Silva Fennica,* 2008, 42(1), 115–124. doi:10.14214/sf.268

Borazan A., Babaç M.T. Morphometry leaf variation in oaks (*Quercus*) of Bolu, Turkey. *Annales Botanici Fennici,* 2003, *40*(40), 233–242.

Bruschi P., Grossoni P., Bussotti F. Within-and among-tree variation in leaf morphology of *Quercus petraea* (Matt.) Liebl. natural populations. *Trees,* 2003, *17*(2), 164–172. doi:10.1007/s00468-002-0218-y

Buck G.W., Bidlack J.E. Identification of *Quercus* and *Celtis* species using morphological and electrophoretic data. *Proceedings of the Oklahoma Academy of Science,* 1998, *78*, 23–33.

Burlacu E., Nisca A., Tanase C. A Comprehensive Review of Phytochemistry and Biological Activities of Quercus Species. *Forests,* 2020, *11*(9), 904. doi:10.3390/f11090904

Bussotti F., Grossoni P. European and Mediterranean oaks (*Quercus* L.; Fagaceae): SEM characterization of the micromorphology of the abaxial leaf surface. *Botanical Journal of the Linnaean Society,* 1997, *124*, 183–199.

Camus A., Les Chênes. Monographie du genre *Quercus* (et *Lithocarpus*). Encyclopédie Économique de Sylviculture. Académie des Sciences. Paris, 1957, 6–8, 182.

Choi Y-E., Harada E., Wada M., Tsuboi H., Morita Y., Kusano T., Sano H. Detoxification of cadmium in tobacco plants: formation and active excretion of crystals containing cadmium and calcium through trichomes. *Planta,* 2001, *213*(1), 45–50. doi:10.1007/s004250000487

Daly R.G., Gastaldo R.A. The effect of leaf orientation to sunlight on stomatal parameters of *Quercus rubra* around the Belgrade lakes, central maine. *Palaios,* 2010, *25*(5-6), 339–346. doi:10.2110/palo.2009.p09-107r

Day T.A., Martin G., Vogelman T.C. Penetration of UV-B radiation in foliage: Evidence that the epidermis behaves as a non-uniform filter. *Plant, Cell & Environment,* 1993, *16*(6), 735–741. doi:10.1111/j.1365-3040.1993.tb00493.x

Deng M., Hipp A., Song Yi-G., Li, Q-Sh., Coombes A., Cotton A. Leaf epidermal features of *Quercus* subgenus Cyclobalanopsis (Fagaceae) and their systematic significance. *Botanical Journal of the Linnean Society,* 2014, *176*(2), 224–259. doi:10.1111/boj.12207

Denk T., Grimmm G.,W., Manos P.S., Deng M., Hipp A. L. An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. In book: *Oaks Physiological Ecology. Exploring the Functional Diversity of Genus Quercus L., Tree Physiology* 2017, *7,* 13–38. doi:10.1007/978-3-319-69099-5_2

Dupouey J.L., Badeau V. Morphological variability of oaks (*Quercus robur* L, *Quercus petraea* (Matt) Liebl, *Quercus pubescens* Willd) in northeastern France: preliminary results. *Annals of Forest Science,* 1993, *50,* 35–40. doi:10.1051/forest:19930702

Dupouey J. L. Analyse multivariable de quelques caracteres morphologiques de populations de chenes (*Quercus robur* L. et *Quercus petraea* (Matt.) Liebl.) du Hurepoix. *Annales de Sciencies Forestières,* 1983, *40*(3), 265–282. doi:10.1051/forest:19830303

Dyal S.C. Akey to the Species of Oaks of Eastern North America Based on Foliage and Twig Characters. *Rhodora,* 1936, *38,* 53–63.

Engel R., Gülz P-G., Herrmann T., Nahrstedtb A. Glandular Trichomes and the Yolatiles Obtained by Steam Distillation of *Quercus robur* Leaves. *Zeitschrift für Naturforschung,* 1993, *48*, 736–744.

European Pharmacopoeia 10.8. Quercus Cortex Monograph– Available from URL: https://pheur.edqm.eu/app/108/content/108.

Evans W.C. Trease and Evans, Pharmacognosy. 9th Edition. Saunders Elsevier 2002; 553–557.

Fiorin L. Spatial coordination between veins and stomata links water supply with water loss in leaves. Università di Padova; 2013.

Fortini P., Marzio P. Di., Pietro R.Di. Differentiation and hybridization of *Quercus frainetto*, *Q. petraea*, and *Q. pubescens* (Fagaceae): insights from macro-morphological leaf traits and molecular data. *Plant Systematics and Evolution,* 2015, *301*(1), 375–385. doi:10.1007/s00606-014-1080-2

Fortini P., Viscosi V., Maiuro L., Fineschi S., Vendramin G.G. Comparative leaf surface morphology and molecular data of five oaks of the subgenus *Quercus* Oerst (Fagaceae). *Plant Biosystems – An International Journal Dealing with All Aspects of Plant Biology,* 2009, *143*(3), 543–554. doi:10.1080/11263500902722980

Foster A.S. Practical Plant Anatomy, 2nd ed. D. Van Nostrand, Princeton. 1949.

Franceschi V.R., Horner H.T. Calcium oxalate crystals in plants. *Botanical Review,* 1980, *46,* 361–427. doi:10.1007/BF02860532

Franceschi V.R., Nakata P.A. Calcium oxalate in plants: formation and function. *Annual Review of Plant Biology,* 2005, *56*(1), 41–71. doi:10.1146/annurev.arplant.56.032604.144106

Gellini R., Bussotti F., Bettin i D., Grossoni P., Bottacci F. Species of the genus *Quercus* in Italy: characterization by means of leaf surface observation. *Giornale botanico italiano,* 1992, *126*(3-4), 481–504.

Gil S.P., Seisdedos L., Reyna M.E., Cerana M.M. Epidermis foliar de tres especies de asteráceas nativas de Argentina con potencial ornamental. *Phyton (B. Aires),* 2012, *81*(2), 205–210.

González-Rodríguez A., Oyama K. Leaf morphometric variation in *Quercus affinis* and *Q. laurina* (Fagaceae), two hybridizing Mexican red oaks. *Botanical Journal of the Linnean Society,* 2005, *147* (4), 427–435. doi:10.1111/j.1095-8339.2004.00394.x

Gülz P-G., Markstädter C., Riederer M. Isomeric alkyl esters in *Quercus robur* leaf cuticular wax. *Phytochemistry,* 1994, *35*(1), 79–81. doi:10.1016/S0031-9422(00)90513-2

Gülz P-G., Müller E., Naturforsch Z. Seasonal Variation in the Composition of Epicuticular Waxes of *Quercus robur* leaves. *Zeitschrift für Naturforschung C,* 1992, *47*, 800–806.

Hardin J.W. Patterns of variation in foliar trichome of eastern North American Quercus. *American Journal of Botany,* 1979a, *66*(5), 576–585.

Hardin J.W. Atlas of Foliar Surface Features in Woody Plants, I. Vestiture and Trichome Types of Eastern North American *Quercus*. *Bulletin of the Torrey Botanical Club,* 1979b, *106*(4): 313–325. doi.org/10.2307/2560358

Hardin J.W. Terminology and Classification of Quercus Trichomes. *Journal of the Elisha Mitchell Scientific Society,* 1976, *92* (4), 151–161.

Hilmarsson H., Traustason B., Kristmundsdottir T., Thormar H. Virucidal activities of medium– and long-chain fatty alcohols and lipids against respiratory syncytial virus and parainfluenza virus type 2: comparison at different pH levels. *Archives of Virology,* 2007, *152*(12), 2225–36. doi:10.1007/s00705-007-1063-5

Hipp A.L., Manos P.S., Hahn M., et al. Genomic landscape of the global oak phylogeny. *New Phytologist,* 2020, *226*(4), 1198-1212. doi:10.1111/nph.16162

Hoof T., Kürschner W.M., Wagner F., Henk V. Stomatal index response of *Quercus robur* and *Quercus petraea* to the anthropogenic atmospheric CO2 increase. *Plant Ecology,* 2005, *183*(2), 237–243.

Ishida T.A, Hattori K., Sato H., Kimura M.T. Differentiation and hybridization between *Quercus crispula* and *Q. dentata* (Fagaceae): insights from morphological traits, amplified fragment length polymorphism markers, and leafminer composition. *American Journal of Botany,* 2003, *90*(5), 769–776. doi:10.3732/ajb.90.5.769

Jankiewicz L.S., Dyki B., Machlańska A., Dubert F. Oak leaf galls: Neuroterus numismalis and *Cynips quercusfolii*, their structure and ultrastructure. *Acta Societatis Botanicorum Poloniae,* 2017, *86*(2), 3537. doi:10.5586/asbp.3537

Jankiewicz L.S., Guzicka M., Marasek-Ciolakowska A. Anatomy and Ultrastructure of Galls Induced by Neuroterus quercusbaccarum (Hymenoptera: Cynipidae) on Oak Leaves (*Quercus robur*). *Insects,* 2021, *12(10)*, 850. doi:10.3390/insects12100850

Jensen R.J., Hokanson S.C., Isebrands J.C., Hancock J.F. Morphometric variation in oaks of the Apostle Islands in Wisconsin: evidence of hybridization between *Quercus rubra* and *Q. ellipsoidalis* (Fagaceae). *American Journal of Botany,* 1993, *80*(11), 1358–1366.

Johansen D.A. Plant Microtechnique. McGraw-Hill, New York, 1940, 523.

Jones J.H. Evolution of the Fagaceae: The Implications of Foliar Features. Annals of Missouri Botanical Garden, 1986, 73, 228-275. doi:10.2307/2399112

Kane C.N., Jordan G.J., Jansen S., McAdam S.A.M. A Permeable Cuticle, Not Open Stomata, Is the Primary Source of Water Loss From Expanding Leaves. *Frontiers in Plant Science,* 2020, *11*. doi:10.3389/fpls.2020.00774

Karabourniotis G., Kofidis G., Fasseas C., Liakoura V., Drossopoulos I. Polyphenol deposition in leaf hairs of *Olea europaea* (Oleaceae) and *Quercus ilex* (Fagaceae). *American Journal of Botany,* 1988, *85*(7), 1007–1012. doi:10.2307/2446367

Kim M.H., Song H.S., Kim C.S. Morphological types andseasonal loss of the trichome of some *Quercus species* in Korea. *Korean Journal of Plant Taxonomy,* 1992, *22*(1), 13–21.

Konovalova O., Omelkovets T., Sydora N., Hurtovenko I., Kalista M., Shcherbakova O. Investigation of the polyphenol composition of red oak (*Quercus rubra* L.) raw materials. *ScienceRise: Pharmaceutical Science,* 2023, *2* (42), 75–81. doi: 10.15587/2519-4852.2023.277969

Kramer P.J., Kozlowski T.T. The physiology of woody plants. San Diego, CA: Academic Press. 1979.

Kraus J.E., de Sousa H.C., Rezende M.H., Castro N.M., Vecchi C., Luque R. Astra Blue and Basic Fuchsin Double Staining of Plant Materials. *Biotechnic & Histochemistry,* 1998, *73*(5), 235–243. doi:10.3109/10520299809141117

Криворучко А., Бессонова В. Показники анатомічної структури листків дуба червоного (Quercus rubra L.) в урботехногенних умовах. *Вісник Львівського університету. Серія біологічна*. 2017. Вип. 76. С. 29–37.

Криворучко А.П., Бессонова В.П. Анатомічна характеристика листків Quercus rubra L. та Quercus robur L. за солітерного та групового зростання. *Ukrainian Journal of Ecology*, 2018, 8(1), 64–71. https://doi.org/10.15421/2017_188

Lattanzio V., Cardinali A., Ruta C., Morone Fortunato I., Lattanzio VMT., Linsalata V., Cicco N. Relationship of secondary metabolism to growth in oregano (*Origanum vulgare* L.) shoot cultures under nutritional stress. *Environmental and Experimental Botany,* 2009, *65*(1), 54–62. doi:10.1016/j.envexpbot.2008.09.002

Lattanzio V., Lattanzio V.M.T., Cardinali A. Role of phenolics in the resistance mechanisms of plants against fungal pathogens and insects. *In: Imperato, F. (org), Phytochemistry: Advances in Research. Research Signposts, Trivandrum,* 2006, *280,* 23–67.

Leiva M.J., Díaz-Maqueda A. Fast-growing seeds and delayed rodent predatory activity in the seeding season: a combined mechanism to escape and survive rodent predation in *Quercus ilex* subsp. ballota L. acorns and seedlings. *Forest Ecology and Management,* 2016, *380*(3), 23–30. doi:10.1016/j.foreco.2016.08.038

Likhanov A.F., Sereda O.V., Gryb V.M., Melnyk V.I., Osadchuk L.S., Yuskevych T. Biochemical markers of vital biodestruction in common oak (*Quercus robur*). *Biosystems Diversity,* 2019, *27*(4), 314–321.

Llamas F., Perez-Morales C., Acedo C., Penas A. Foliar trichomes of the evergreen and semi-deciduous species of the genus *Quercus* (Fagaceae) in the Iberian Peninsula. *Botanical Journal of the Linnean Society,* 1955, *117*(1), 47–57. doi:10.1111/j.1095-8339.1995.tb02377.x

Lou Y., Zhou Z.K. Leaf epidermis of *Quercus subgen*. Cyclobalanopsis (Orest.) Schneid. (Fagaceae). *Journal of Systematics and Evolution,* 2001, *39*(6), 489–501.

Martins J.P.R., Wawrzyniak M.K., Ley-López J.M., Kalemba E.M., Mendes M.M., Chmielarz P. 6-Benzylaminopurine and kinetin modulations during in vitro propagation of *Quercus robur* (L.): an assessment of anatomical, biochemical, and physiological profiling of shoots. *Plant Cell Tissue and Organ Culture,* 2022, *151*(1), 1–16.

Masson G., Puech J-L., Moutounet M. Localization of the ellagitannins in the tissues of *Quercus robur* and *Quercus petraea* woods. *Phytochemistry,* 1994, *37*(5), 1245–1249. doi:10.1016/S0031-9422(00)90392-3

Matthew E. Ward Cline Anatomical and Physiological Responses of *Quercus agrifolia* to Changes in Climate from the Late Pleistocene to the Present-Day, 2022. URL: http://hdl.handle.net/20.500.12680/1544bw05t

Meidner H., Mansfield T.A. Physiology of stomata. McGraw Hill, London. 1968.

Meric C. Calcium oxalate crystals in some species of the tribe Inuleae (Asteraceae). *Acta biologica Cracoviensia. Series botanica,* 2009, *51*(1), 105–110. doi:10.17129/botsci.259

Mitrović M., Pavlović P., Popović R. Morphoanatomical leaf characteristics of *Quercus robur* L. and Pinus nigra Arn. from urban and rural habitats. Proceedings of the 3rd international conference on the development of forestry and wood science/technology. Belgrade Mt. Goč Serbia Yugoslavia (II). 1997. 305–312.

Morales D. Oak trees (*Quercus* spp.) as a source of extracts with biological activities: A narrative review. *Trends in Food Science & Technology,* 2021, *109,* 116–125. doi:10.1016/j.tifs.2021.01.029

Muhammad S., Wuyts K., Nuyts G., De Wael K., Samson R. Characterization of epicuticular wax structures on leaves of urban plant species and its association with leaf wettability. *Urban Forestry & Urban Greening,* 2020, *47,* 126557. doi:10.1016/j.ufug.2019.126557

Nagel L.M., Bassmanb J.H., Edwards G.E., Robberecht R., Franceshi V.R. Leaf anatomical changes in Populus trichocarpa, Quercus rubra, Pseudotsuga menziesii and Pinus ponderosa exposed to enhanced ultraviolet-B radiation. *Physiologia Plantarum,* 1998, *104*(3), 385–396. doi:10.1034/j.1399-3054.1998.1040314.x

Nikolić N., Merkulov L.J., Pajević S., Krstić B. Variability of Leaf Anatomical Characteristics in Pedunculate Oak Genotypes (*Quercus robur* L.). Proceedings of the Balkan Scientific Conference of Biology, Plovdiv, 2005, 240–247.

Nikolić N.P., Krstić B.D., Pajević S.P., Orlović S.S. Variability of leaf characteristics in different pedunculate oak genotypes (*Quercus robur* L.). *Zbornik Matice Srpske za Prirodne Nauke Matica Srpska Journal for Natural Sciences,* 2006, *110,* 95–105. doi:10.2298/ZMSPN0611095N

Nixon K.C. Infrageneric Classification of *Quercus* (Fagaceae) and Typification of Sectional Names. *Annales des Sciences Forestières,* 1993, *50* (1), 25–34.

Nobrega M.C., Pereira S.J. Gradients of anatomy and morphology of leaves in the crowns of cork oak. *Scientia gerundensis,* 1992, *18,* 53–60.

Panahi P., Jamzad Z., Pourmajidian M.R., Fallah A., Pourhashemi M. Foliar epidermis morphology in *Quercus* (subgenus *Quercus*, section *Quercus*). *Acta Botanica Croatica,* 2012, *71*(1), 95–113. doi:10.2478/v10184-010-0029-y

Paul V., Sharma L., Pandey R., Meena R.C. Measurement of Stomatal Density and Stomatal Index on Leaf/Plant Surfaces. *Manual of ICAR sponsored training programme on "Physiological Techniques to Analyze the Impact of Climate change on crop plants". Division of Plant Physiology IARI, New Delhi, India,* 2017, 27–30.

Penas A., Llamas F., Pérez Morales C. y Acedo C. Aportaciones al conocimiento del género *Quercus* en la cordillera cantábrica: I. Tricomas foliares de las especies caducifolias. *Lagascalia,* 1994, *17* (2), 311–324.

Pérez A.J., Pecio Ł., Kowalczyk M., Kontek R., Gajek G., Stopinsek L., Stochmal A. Triterpenoid Components from Oak Heartwood (*Quercus robur*) and Their Potential Health Benefits. *Journal of Agricultural and Food Chemistry,* 2017, *65*(23), 4611–4623. doi:10.1021/acs.jafc.7b01396

Petrovic S., Sobajic S., Rakic S., Tomic A., Kukic J. Investigation of kernel oils of *Quercus robur* and *Quercus cerris*. *Chemistry of Natural Compounds,* 2004, *40*, 420–422. doi:10.1007/s10600-005-0003-4

Plainfossé H., Burger P., Azoulay S., Landreau A., Verger-Dubois G., Fernandez X. Development of a Natural Anti-Age Ingredient Based on *Quercus* pubescens Willd. Leaves Extract — A Case Study. *Cosmetics,* 2018, *5*(1), 15. doi:10.3390/cosmetics5010015

Prasad R.B.N., Gülz P-G. Surface Structure and Chemical Composition of Leaf Waxes from *Quercus robur* L., Acer pseudoplatanus L. and Jug Ians regia L. *Zeitschrift fur Naturforschung C,* 1990, *45*(7), 813–817. doi:10.1515/znc-1990-7-811

Rafii Z.A., Dodd R.S., Pellau Y. Mediterraneal Overgreen Oak Diversity: Morphological and Chemical Variations of Acors. *Canadian Journal of Botany,* 1993, *70*(7), 1459–1466. doi:10.1139/b92-184

Río S., Álvarez R., Candelas A., González-Sierra S., Herrero L., Penas A. Preliminary Study on Taxonomic Review Using Histological Sections of Some Iberian Species from the Genus *Quercus* L. (Fagaceae). *American Journal of Plant Sciences,* 2014, *5*, 2773–2784. doi:10.4236/ajps.2014.518294

Rotondi A., Rossi F., Asunis C., Cesaraccio C. Leaf xeromorphic adaptations of some plants of a coastal Mediterranean macchia ecosystem. *Journal of Mediterranean Ecology,* 2003, *4* (3–4), 25–35.

Burns R.M., Honkala B.H. Silvics of North America: 2. Hardwoods. Agriculture Handbook 654, USDA Forest Service, Washington DC. 1990.

Sass J.E. Botanical Microtechnique, 2nd ed. Iowa State College, Ames. 1951.

Scareli-Santos C., Herrera-Arroyo M.L., Sanchez-Mondragon M.L., Gonzalez-Rodriguez A., Bacon J., Oyama K. Comparative analysis of micromorphological characters in two distantly related Mexican oaks, *Quercus conzattii* and *Q. eduardii* (Fagaceae) and their hybrids. *Brittonia,* 2007, *59*, 37–48. doi:10.1663/0007-196X(2007)59[37:CAOMCI]2.0.CO;2

Schicchi R., Mazzola P. and Raimondo F.M. Eco-Morphologic and Taxonomic Studies of *Quercus Hybrids* (Fagaceae) in Sicily. *Bocconea,* 2001, *13*, 485–490.

Sevillano I., Short I., Grant J., O'Reilly C. Effects of light availability on morphology, growth and biomass allocation of *Fagus sylvatica* and *Quercus robur* seedlings. *Forest Ecology and Management,* 2016, *374*, 11–19. doi:10.1016/j.foreco.2016.04.048

Sha Valli Khan P.S., Evers D., Hausman J.F. Stomatal Characteristics and Water Relations of In Vitro Grown *Quercus robur* NL 100 in Relation to Acclimatization. *Silvae Genetica,* 1999, *48* (2), 83–87.

Shahbaz S. E., Abdulrahman S. S., Abdulrahman H. A. Use of Leaf Anatomy for Identification of *Quercus* L. Species Native to Kurdistan-Iraq. Science Journal of University of Zakho, 2015, 3(2), 222–232. Retrieved from https://sjuoz.uoz.edu.krd/index.php/sjuoz/article/view/146

Simões R., Rodrigues A., Ferreira-Dias S., Miranda I., Pereira H. Chemical Composition of Cuticular Waxes and Pigments and Morphology of Leaves of *Quercus suber* Trees of Different Provenance. *Plants,* 2020, *9*(9), 1165. doi:10.3390/plants9091165

Sohretoglu D., Renda G. The polyphenolic profile of Oak (*Quercus*) species: a phytochemical and pharmacological overview. *Phytochemistry Reviews,* 2020, *19*(6), 1379–1426. doi:10.1007/s11101-020-09707-3

Spellenberg R., Bacon J.R. Taxonomy and Distribution of a Natural Group of Black Oaks of Mexico (*Quercus*, Section *Lobatae*, Subsection Racemiflorae). *Systematic Botany,* 1996, *21*(1), 85–99.

Tanase C., Nicolescu A., Nisca A.. Stefănescu R., Babotă M., Mare A.D., Ciurea C.N., Man A. Biological Activity of Bark Extracts from Northern Red Oak (*Quercus rubra* L.): An Antioxidant, Antimicrobial and Enzymatic Inhibitory Evaluation. *Plants,* 2022, *11*(18), 2357. doi:10.3390/plants11182357

Thomson P.M., Mohlenbrock R.H. Foliar Trichomes of *Quercus* in the Eastern United States. *Journal of the Arnold Arboretum,* 1979, *60*(3), 350–366.

Top S.M., Preston C.M., Dukes J.S., Tharayil N. Climate Influences the Content and Chemical Composition of Foliar Tannins in Green and Senesced Tissues of *Quercus rubra*. *Frontiers in Plant Science,* 2017, *8*, 423. doi: 10.3389/fpls.2017.00423

Tschan G.F., Denk T. Trichome types, foliar indumentum and epicuticular wax in the Mediterranean gall oaks, *Quercus* subsection *Galliferae* (Fagaceae): implications for taxonomy, ecology and evolution. *Botanical Journal of the Linnean Society,* 2012, *169*(4), 611–644. doi:10.1111/j.1095-8339.2012.01233.x

Turner N.C., Heichel G.H. Stomatal Development and Seasonal Changes in Diffusive Resistance of Primary and Regrowth Foliage of Red Oak (*Quercus rubra* L.) and Red Maple (*Acer rubrum* L.). *New Phytologist,* 1977, *78*(1), 71–81. doi:10.1111/j.1469-8137.1977.tb01544.x

Uzunova K., Palamarev E., Ehrendorfer F. Anatomical changes and evolutionary trends in the foliar epidermis of extant and fossil Euro-Mediterranean oaks (Fagaceae). *Plant Systematics and Evolution,* 1997, *204*(3/4), 141–159.

Uzunova K., Palamarev E. An Investigation of the Leaf Epidermis of the European (Non-Balkan) Species of the Genus *Quercus*. *Fitologia,* 1993, *45*, 3–15.

Valencia S., Delgado A. Los tricomas foliares en la caracterización de un grupo de especies del género *Quercus*, sección (Fagaceae). *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Botánica,* 2003, *74*(1),5–15.

Valladares F., Chico J.M., Aranda I., Balaguer L., Dizengremel P., Manrique E. and Dreyer E. The Greater Seedling High-Light Tolerance of *Quercus robur* over Fagus sylvatica Is Linked to a Greater Physiological Plasticity. *Trees,* 2002, *16*, 395–403.

Volin P. Analysis of steroidal lipids by gas and liquid chromatography. *Journal of Chromatography A,* 2001, *935*(1-2), 125–40. doi:10.1016/S0021-9673(01)01089-5

Xavier S.K., Devkar R.A., Chaudhary S., Shreedhara C.S., Setty M.M. Pharmacognostical standardization and HPTLC Quantification of Gallic acid in Homonoia riparia Lour. *Pharmacognosy Journal,* 2015, *7*(6), 383–388. doi:10.5530/pj.2015.6.12

Yiotis C., Manetas Y., Psaras G.K. Leaf and green stem anatomy of the drought deciduous Mediterranean shrub *Calicome villosa* (Poiret) Link. (Leguminosae). *Flora,* 2006, *201*(2), 102–107. doi:10.1016/j.flora.2005.04.007

Yücedağ C., Sanders J., Musah M., Gailing O. Stomatal density in *Quercus petraea* and *Q. robur* natural populations in Northern Turkey. *Dendrobiology,* 2019, *81*, 58–64. doi:10.12657/denbio.081.007

Zhou Z.K., Wilkinson H., Wu Z.Y. Taxonomical and evolutionary implications of the leaf anatomy and architecture of *Quercus* L. subgenus *Quercus* from China. *Cathaya,* 1995, *7*, 1–34.

REFERENCES

Abrams, M.D., & Kubiske, M.E. (1990). Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: Influene of light regime and shade-tolerance rank. *Forest Ecology and Management, 31*(4), 245–253. doi:10.1016/0378-1127(90)90072-J

Ashton, P.M.S., & Berlyn, G.P. (1994). A comparison of leaf physiology and anatomy of *Quercus* (section *Erythrobalanus* – Fagaceae) species in different light environments *American Journal of Botany, 81*(5), 589–597. doi:10.2307/2445734

Bačić, T., & Miličić D. (1985). Contribution to the leaf anatomy of *Quercus Ilex* L. *Acta Botanica Croatica, 44*, 23–31.

Bačić, T. (1981). Investigations of stomata of three oak species with light and scanning electron microscope. *Acta Botánica Croatia, 40,* 85–90.

Bahamonde, H.A., Gil, L., & Fernández, V. (2018). Surface. Properties and permeability to calcium chloride of *Fagus sylvatica* and *Quercus petraea* leaves of different canopy heights. *Frontiers in Plant Science, 9,* 494. doi: 10.3389/fpls.2018.00494

Barthlott, W., Neinhuis, C., Cutler, D., Ditsch, F., Meusel, I., Theisen, I., & Wilhelmi, H. (1998). Classification and Terminology of Plant Epicuticular Waxes. *Botanical Journal of the Linnean Society, 126*(3), 237–260. doi: 10.1111/j.1095-8339.1998.tb02529.x

Batos, B., Vilotic, D., Orlovic, S., & Miljkovic, D. (2010). Inter and intra-population variation of leaf stomatal traits of *Quercus robur* L. in Northern Serbia. *Archives of Biological Sciences, 62*(4), 1125–1136. doi:10.2298/ABS1004125B

Berlyn, G.P., & Miksche, J.P. (1976). Botanical Microtechnique and Cytochemistry. *Ames: Iowa State University Press,* 1256–1231.

Boratynski, A., Marcysiak, K., Lewandowska, A., Jasinska, A., Iszkulo, G., & Burczyk, J. (2008). Differences in leaf morphology between *Quercus petraea* and *Q. robur* adult and young individuals. *Silva Fennica, 42*(1), 115–124. doi:10.14214/sf.268

Borazan, A., & Babaç, M.T. (2003). Morphometry leaf variation in oaks (*Quercus*) of Bolu, Turkey. *Annales Botanici Fennici, 40*(40), 233–242.

Bruschi, P., Grossoni, P., & Bussotti, F. (2003). Within-and among-tree variation in leaf morphology of *Quercus petraea* (Matt.) Liebl. natural populations. *Trees, 17*(2), 164–172. doi:10.1007/s00468-002-0218-y

Buck, G.W., & Bidlack, J.E. (1998). Identification of *Quercus* and *Celtis* species using morphological and electrophoretic data. *Proceedings of the Oklahoma Academy of Science,78*, 23–33.

Burlacu, E., Nisca, A., & Tanase, C. (2020). A Comprehensive Review of Phytochemistry and Biological Activities of Quercus Species. *Forests, 11*(9), 904. doi:10.3390/f11090904

Bussotti, F., & Grossoni, P. (1997). European and Mediterranean oaks (*Quercus* L.; Fagaceae): SEM characterization of the micromorphology of the abaxial leaf surface. *Botanical Journal of the Linnaean Society, 124*, 183–199.

Camus, A., & Les Chênes. (1957). Monographie du genre *Quercus* (et *Lithocarpus*). Encyclopédie Économique de Sylviculture. Académie des Sciences. Paris, 6–8, 182.

Choi, Y-E., Harada, E., Wada, M., Tsuboi, H., Morita, Y., Kusano, T., & Sano, H. (2001). Detoxification of cadmium in tobacco plants: formation and active excretion of crystals containing cadmium and calcium through trichomes. *Planta, 213*(1), 45–50. doi:10.1007/s004250000487

Daly, R.G., & Gastaldo, R.A. (2010). The effect of leaf orientation to sunlight on stomatal parameters of *Quercus rubra* around the Belgrade lakes, central maine. *Palaios, 25*(5-6), 339–346. doi:10.2110/palo.2009.p09-107r

Day, T.A., Martin, G., & Vogelman, T.C. (1993). Penetration of UV-B radiation in foliage: Evidence that the epidermis behaves as a non-uniform filter. *Plant, Cell & Environment, 16*(6), 735–741. doi:10.1111/j.1365-3040.1993.tb00493.x

Deng, M., Hipp, A., Song, Yi-G., Li, Q-Sh., Coombes, A., & Cotton, A. (2014). Leaf epidermal features of *Quercus* subgenus Cyclobalanopsis (Fagaceae) and their systematic significance. *Botanical Journal of the Linnean Society,176*(2), 224–259. doi:10.1111/boj.12207

Denk, T., Grimmm G.,W., Manos, P.S., Deng, M., & Hipp, A.L. (2017). An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. In book: *Oaks Physiological Ecology. Exploring the Functional Diversity of Genus Quercus L., Tree Physiology 7,* 13–38. doi:10.1007/978-3-319-69099-5_2

Dupouey, J.L., & Badeau, V. (1993). Morphological variability of oaks (*Quercus robur* L, *Quercus petraea* (Matt) Liebl, *Quercus pubescens* Willd) in northeastern France: preliminary results. *Annals of Forest Science, 50,* 35–40. doi:10.1051/forest:19930702

Dupouey, J.L. (1983). Analyse multivariable de quelques caracteres morphologiques de populations de chenes (*Quercus robur* L. et *Quercus petraea* (Matt.) Liebl.) du Hurepoix. *Annales de Sciencies Forestières, 40*(3), 265–282. doi:10.1051/forest:19830303

Dyal, S.C. (1936). Akey to the Species of Oaks of Eastern North America Based on Foliage and Twig Characters. *Rhodora, 38,* 53–63.

Engel, R., Gülz, P-G., Herrmann, T., & Nahrstedtb, A. (1993). Glandular Trichomes and the Yolatiles Obtained by Steam Distillation of *Quercus robur* Leaves. *Zeitschrift für Naturforschung, 48*, 736–744.

European Pharmacopoeia 10.8. Quercus Cortex Monograph– Available from URL: https://pheur.edqm.eu/app/108/content/108.

Evans, W.C. (2002). Trease and Evans, Pharmacognosy. 9th Edition. Saunders Elsevier 553–557.

Fiorin, L. (2013). Spatial coordination between veins and stomata links water supply with water loss in leaves. Università di Padova.

Fortini, P., Marzio, P. Di., Pietro, & R.Di. (2015). Differentiation and hybridization of *Quercus frainetto*, *Q. petraea*, and *Q. pubescens* (Fagaceae): insights from macro-morphological leaf traits and molecular data. *Plant Systematics and Evolution, 301*(1), 375–385. doi:10.1007/s00606-014-1080-2

Fortini, P., Viscosi, V., Maiuro, L., Fineschi, S., & Vendramin, G.G. (2009). Comparative leaf surface morphology and molecular data of five oaks of the subgenus *Quercus* Oerst (Fagaceae). *Plant Biosystems – An International Journal Dealing with All Aspects of Plant Biology, 143*(3), 543–554. doi:10.1080/11263500902722980

Foster, A.S.(1949). Practical Plant Anatomy, 2nd ed. D. Van Nostrand, Princeton.

Franceschi, V.R., & Horner, H.T. (1980). Calcium oxalate crystals in plants. *Botanical Review, 46,* 361–427. doi:10.1007/BF02860532

Franceschi, V.R., & Nakata, P.A. (2005). Calcium oxalate in plants: formation and function. *Annual Review of Plant Biology, 56*(1), 41–71. doi:10.1146/annurev.arplant.56.032604.144106

Gellini, R., Bussotti, F., Bettin,i D., Grossoni, P., & Bottacci, F. (1992). Species of the genus *Quercus* in Italy: characterization by means of leaf surface observation. *Giornale botanico italiano, 126*(3-4), 481–504.

Gil, S.P., Seisdedos, L., Reyna, M.E., & Cerana, M.M. (2012). Epidermis foliar de tres especies de asteráceas nativas de Argentina con potencial ornamental. *Phyton (B. Aires), 81*(2), 205–210.

González-Rodríguez, A., & Oyama, K. (2005). Leaf morphometric variation in *Quercus affinis* and *Q. laurina* (Fagaceae), two hybridizing Mexican red oaks. *Botanical Journal of the Linnean Society, 147* (4), 427–435. doi:10.1111/j.1095-8339.2004.00394.x

Gülz, P-G., Markstädter, C., & Riederer, M. (1994). Isomeric alkyl esters in *Quercus robur* leaf cuticular wax. *Phytochemistry, 35*(1), 79–81. doi:10.1016/S0031-9422(00)90513-2

Gülz, P-G., Müller, E., & Naturforsch, Z. (1992). Seasonal Variation in the Composition of Epicuticular Waxes of *Quercus robur* leaves. *Zeitschrift für Naturforschung C, 47*, 800–806.

Hardin, J.W. (1979b). Atlas of Foliar Surface Features in Woody Plants, I. Vestiture and Trichome Types of Eastern North American *Quercus*. *Bulletin of the Torrey Botanical Club, 106*(4): 313–325. doi.org/10.2307/2560358

Hardin, J.W. (1979a). Patterns of variation in foliar trichome of eastern North American Quercus. *American Journal of Botany,66*(5), 576–585.

Hardin, J.W. (1976). Terminology and Classification of Quercus Trichomes. *Journal of the Elisha Mitchell Scientific Society, 92* (4), 151–161.

Hilmarsson, H., Traustason, B., Kristmundsdottir, T., & Thormar, H. (2007). Virucidal activities of medium– and long-chain fatty alcohols and lipids against respiratory syncytial virus and parainfluenza virus type 2: comparison at different pH levels. *Archives of Virology, 152*(12), 2225–36. doi:10.1007/s00705-007-1063-5

Hipp, A.L., Manos, P.S., Hahn, M., et al. (2020). Genomic landscape of the global oak phylogeny. *New Phytologist, 226*(4), 1198–1212. doi:10.1111/nph.16162

Hoof, T., Kürschner, W.M., Wagner, F., & Henk, V. (2005). Stomatal index response of *Quercus robur* and *Quercus petraea* to the anthropogenic atmospheric CO2 increase. *Plant Ecology, 183*(2), 237–243.

Ishida, T.A, Hattori, K., Sato, H., & Kimura, M.T. (2003). Differentiation and hybridization between *Quercus crispula* and *Q. dentata* (Fagaceae): insights from morphological traits, amplified fragment length polymorphism markers, and leafminer composition. *American Journal of Botany, 90*(5), 769–776. doi:10.3732/ajb.90.5.769

Jankiewicz, L.S., Dyki, B., Machlańska, A., & Dubert, F. (2017). Oak leaf galls: Neuroterus numismalis and *Cynips quercusfolii*, their structure and ultrastructure. *Acta Societatis Botanicorum Poloniae, 86*(2), 3537. doi:10.5586/asbp.3537

Jankiewicz, L.S., Guzicka, M., & Marasek-Ciolakowska, A. (2021). Anatomy and Ultrastructure of Galls Induced by Neuroterus quercusbaccarum (Hymenoptera: Cynipidae) on Oak Leaves (*Quercus robur*). *Insects, 12(10)*, 850. doi:10.3390/insects12100850

Jensen, R.J., Hokanson, S.C., Isebrands, J.C., & Hancock, J.F. (1993). Morphometric variation in oaks of the Apostle Islands in Wisconsin: evidence of hybridization between *Quercus rubra* and *Q. ellipsoidalis* (Fagaceae). *American Journal of Botany, 80*(11), 1358–1366.

Johansen, D.A. (1940). Plant Microtechnique. McGraw-Hill, New York, 523.

Jones, J.H. (1986) Evolution of the Fagaceae: The Implications of Foliar Features. Annals of Missouri Botanical Garden, 73, 228–275. doi:10.2307/2399112

Kane, C.N., Jordan, G.J., Jansen, S., & McAdam, S.A.M. (2020). A Permeable Cuticle, Not Open Stomata, Is the Primary Source of Water Loss From Expanding Leaves. *Frontiers in Plant Science, 11*. doi:10.3389/fpls.2020.00774

Karabourniotis, G., Kofidis, G., Fasseas, C., Liakoura, V., & Drossopoulos, I. (1988). Polyphenol deposition in leaf hairs of *Olea europaea* (Oleaceae) and *Quercus ilex* (Fagaceae). *American Journal of Botany, 85*(7), 1007–1012. doi:10.2307/2446367

Kim, M.H., Song, H.S., & Kim, C.S. (1992). Morphological types andseasonal loss of the trichome of some *Quercus species* in Korea. *Korean Journal of Plant Taxonomy, 22*(1), 13–21.

Konovalova, O., Omelkovets, T., Sydora, N., Hurtovenko, I., Kalista, M., & Shcherbakova, O. (2023). Investigation of the polyphenol composition of red oak (*Quercus rubra* L.) raw materials. *ScienceRise: Pharmaceutical Science, 2* (42), 75–81. doi: 10.15587/2519-4852.2023.277969

Kramer, P.J., & Kozlowski, T.T. (1979). The physiology of woody plants. San Diego, CA: Academic Press.

Kraus, J.E., de Sousa, H.C., Rezende, M.H., Castro, N.M., Vecchi, C., & Luque, R. (1998). Astra Blue and Basic Fuchsin Double Staining of Plant Materials. *Biotechnic & Histochemistry, 73*(5), 235–243. doi:10.3109/10520299809141117

Kryvoruchko, A., & Bessonova, V. (2017). Indicators of the anatomical structure of red oak (*Quercus rubra* L.) leaves in urbotechnogenic conditions. *Visnyk of the Lviv University. Series Biology,76*, 29–37. doi:10.30970/vlubs.2017.76.04 (in Ukrainian).

Kryvoruchko, A.P., & Bessonova, V.P. (2018). Anatomical characteristics of leaves of *Quercus rubra* L. and *Quercus robur* L. during solitary and group growth. *Ukrainian Journal of Ecology, 8*(1), 64–71 (in Ukrainian).

Lattanzio, V., Cardinali, A., Ruta, C., Morone Fortunato, I., Lattanzio, VMT., Linsalata, V., & Cicco, N. (2009). Relationship of secondary metabolism to growth in oregano (*Origanum vulgare* L.) shoot cultures under nutritional stress. *Environmental and Experimental Botany, 65*(1), 54–62. doi:10.1016/j.envexpbot.2008.09.002

Lattanzio, V., Lattanzio, V.M.T., & Cardinali, A. (2006). Role of phenolics in the resistance mechanisms of plants against fungal pathogens and insects. *In: Imperato, F. (org), Phytochemistry: Advances in Research. Research Signposts, Trivandrum,280*,23–67.

Leiva, M.J., & Díaz-Maqueda, A. (2016). Fast-growing seeds and delayed rodent predatory activity in the seeding season: a combined mechanism to escape and survive rodent predation in *Quercus ilex* subsp. ballota L. acorns and seedlings. *Forest Ecology and Management, 380*(3), 23–30. doi:10.1016/j.foreco.2016.08.038

Likhanov, A.F., Sereda, O.V., Gryb, V.M., Melnyk, V.I., Osadchuk, L.S., & Yuskevych, T. (2019). Biochemical markers of vital biodestruction in common oak (*Quercus robur*). *Biosystems Diversity, 27*(4), 314–321.

Llamas, F., Perez-Morales, C., Acedo, C., & Penas, A. (1955). Foliar trichomes of the evergreen and semi-deciduous species of the genus *Quercus* (Fagaceae) in the Iberian Peninsula. *Botanical Journal of the Linnean Society, 117*(1), 47–57. doi:10.1111/j.1095-8339.1995.tb02377.x

Lou, Y., & Zhou, Z.K. (2001). Leaf epidermis of *Quercus subgen*. Cyclobalanopsis (Orest.) Schneid. (Fagaceae). *Journal of Systematics and Evolution, 39*(6), 489–501.

Martins, J.P.R., Wawrzyniak, M.K., Ley-López, J.M., Kalemba, E.M., Mendes, M.M., & Chmielarz, P. (2022). 6-Benzylaminopurine and kinetin modulations during in vitro propagation of *Quercus robur* (L.): an assessment of anatomical, biochemical, and physiological profiling of shoots. *Plant Cell Tissue and Organ Culture, 151*(1),1–16.

Masson, G., Puech, J-L., & Moutounet, M. (1994). Localization of the ellagitannins in the tissues of *Quercus robur* and *Quercus petraea* woods. *Phytochemistry, 37*(5), 1245–1249. doi:10.1016/S0031-9422(00)90392-3

Matthew, E. (2022). Ward Cline Anatomical and Physiological Responses of *Quercus agrifolia* to Changes in Climate from the Late Pleistocene to the Present-Day, http://hdl.handle.net/20.500.12680/1544bw05t

Meidner, H., & Mansfield, T.A. (1968). Physiology of stomata. McGraw Hill, London.

Meric, C. (2009). Calcium oxalate crystals in some species of the tribe Inuleae (Asteraceae). *Acta biologica Cracoviensia. Series botanica, 51*(1), 105–110. doi:10.17129/botsci.259

Mitrović, M., Pavlović, P., & Popović, R. (1997). Morphoanatomical leaf characteristics of *Quercus robur* L. and Pinus nigra Arn. from urban and rural habitats. Proceedings of the 3rd international conference on the development of forestry and wood science/technology. Belgrade Mt. Goč Serbia Yugoslavia (II). 305–312.

Morales, D. (2021). Oak trees (*Quercus* spp.) as a source of extracts with biological activities: A narrative review. *Trends in Food Science & Technology, 109*, 116–125. doi:10.1016/j.tifs.2021.01.029

Muhammad, S., Wuyts, K., Nuyts, G., De Wael K., & Samson, R. (2020). Characterization of epicuticular wax structures on leaves of urban plant species and its association with leaf wettability. *Urban Forestry & Urban Greening, 47*, 126557. doi:10.1016/j.ufug.2019.126557

Nagel, L.M., Bassmanb, J.H., Edwards, G.E., Robberecht, R., & Franceshi, V.R. (1998). Leaf anatomical changes in Populus trichocarpa, Quercus rubra, Pseudotsuga menziesii and Pinus ponderosa exposed to enhanced ultraviolet-B radiation. *Physiologia Plantarum, 104*(3), 385–396. doi:10.1034/j.1399-3054.1998.1040314.x

Nikolić, N., Merkulov, L.J., Pajević, S., & Krstić, B. (2005). Variability of Leaf Anatomical Characteristics in Pedunculate Oak Genotypes (*Quercus robur* L.). Proceedings of the Balkan Scientific Conference of Biology, Plovdiv, , 240–247.

Nikolić, N.P., Krstić, B.D., Pajević, S.P., & Orlović, S.S. (2006). Variability of leaf characteristics in different pedunculate oak genotypes (*Quercus robur* L.). *Zbornik Matice Srpske za Prirodne Nauke Matica Srpska Journal for Natural Sciences, 110,* 95–105. doi:10.2298/ZMSPN0611095N

Nixon, K.C. (1993). Infrageneric Classification of *Quercus* (Fagaceae) and Typification of Sectional Names. *Annales des Sciences Forestières, 50* (1), 25–34.

Nobrega, M.C., & Pereira, S.J. (1992). Gradients of anatomy and morphology of leaves in the crowns of cork oak. *Scientia gerundensis, 18,* 53–60.

Panahi, P., Jamzad, Z., Pourmajidian, M.R., Fallah, A., & Pourhashemi, M. (2012). Foliar epidermis morphology in *Quercus* (subgenus *Quercus*, section *Quercus*). *Acta Botanica Croatica, 71*(1), 95–113. doi:10.2478/v10184-010-0029-y

Paul, V., Sharma, L., Pandey, R., & Meena, R.C. (2017). Measurement of Stomatal Density and Stomatal Index on Leaf/Plant Surfaces. *Manual of ICAR sponsored training programme on "Physiological Techniques to Analyze the Impact of Climate change on crop plants". Division of Plant Physiology IARI, New Delhi, India,* 27–30.

Penas, A., Llamas, F., Pérez Morales, C. y Acedo, C. (1994). Aportaciones al conocimiento del género *Quercus* en la cordillera cantábrica: I. Tricomas foliares de las especies caducifolias. *Lagascalia, 17* (2), 311–324.

Pérez, A.J., Pecio, Ł., Kowalczyk, M., Kontek, R., Gajek, G., Stopinsek, L., & Stochmal, A. (2017). Triterpenoid Components from Oak Heartwood (*Quercus robur*) and Their Potential Health Benefits. *Journal of Agricultural and Food Chemistry, 65*(23), 4611–4623. doi:10.1021/acs.jafc.7b01396

Petrovic, S., Sobajic, S., Rakic, S., Tomic, A., & Kukic, J. (2004). Investigation of kernel oils of *Quercus robur* and *Quercus cerris*. *Chemistry of Natural Compounds, 40*, 420–422. doi:10.1007/s10600-005-0003-4

Plainfossé, H., Burger, P., Azoulay, S., Landreau, A., Verger-Dubois, G., & Fernandez, X. (2018). Development of a Natural Anti-Age Ingredient Based on *Quercus* pubescens Willd. Leaves Extract — A Case Study. *Cosmetics, 5*(1), 15. doi:10.3390/cosmetics5010015

Prasad, R.B.N., & Gülz, P-G. (1990). Surface Structure and Chemical Composition of Leaf Waxes from *Quercus robur* L., Acer pseudoplatanus L. and Jug Ians regia L. *Zeitschrift fur Naturforschung C, 45*(7), 813–817. doi:10.1515/znc-1990-7-811

Rafii, Z.A., Dodd, R.S., & Pellau, Y. (1993). Mediterraneal Overgreen Oak Diversity: Morphological and Chemical Variations of Acors. *Canadian Journal of Botany, 70*(7), 1459–1466. doi:10.1139/b92-184

Río, S., Álvarez, R., Candelas, A., González-Sierra, S., Herrero, L., & Penas, A. (2014). Preliminary Study on Taxonomic Review Using Histological Sections of Some Iberian Species from the Genus *Quercus* L. (Fagaceae). *American Journal of Plant Sciences, 5*, 2773–2784. doi:10.4236/ajps.2014.518294

Rotondi, A., Rossi, F., Asunis, C., & Cesaraccio, C. (2003). Leaf xeromorphic adaptations of some plants of a coastal Mediterranean macchia ecosystem. *Journal of Mediterranean Ecology, 4* (3–4), 25–35.

Burns, R.M., & Honkala, B.H. (1990). Silvics of North America: 2. Hardwoods. Agriculture Handbook 654, USDA Forest Service, Washington DC.

Sass, J.E. (1951). Botanical Microtechnique, 2nd ed. Iowa State College, Ames.

Scareli-Santos, C., Herrera-Arroyo, M.L., Sanchez-Mondragon, M.L., Gonzalez-Rodriguez, A., Bacon, J., & Oyama, K. (2007). Comparative analysis of micromorphological characters in two distantly related Mexican oaks, *Quercus conzattii* and *Q. eduardii* (Fagaceae) and their hybrids. *Brittonia, 59*, 37–48. doi:10.1663/0007-196X(2007)59[37:CAOMCI]2.0.CO;2

Schicchi, R., Mazzola, P., & Raimondo, F.M. (2001) Eco-Morphologic and Taxonomic Studies of *Quercus Hybrids* (Fagaceae) in Sicily. *Bocconea, 13*, 485–490.

Sevillano, I., Short, I., Grant, J., & O'Reilly, C. (2016). Effects of light availability on morphology, growth and biomass allocation of *Fagus sylvatica* and *Quercus robur* seedlings. *Forest Ecology and Management, 374*, 11–19. doi:10.1016/j.foreco.2016.04.048

Sha Valli Khan, P.S., Evers, D., & Hausman, J.F. (1999). Stomatal Characteristics and Water Relations of In Vitro Grown *Quercus robur* NL 100 in Relation to Acclimatization. *Silvae Genetica, 48* (2), 83–87.

Shahbaz, S.E., Abdulrahman, S.S., & Abdulrahman, H.A. (2015). Use of Leaf Anatomy for Identification of *Quercus* L. Species Native to Kurdistan-Iraq. Science Journal of University of Zakho, 3(2), 222–232. Retrieved from https://sjuoz.uoz.edu.krd/index.php/sjuoz/article/view/146

Simões, R., Rodrigues, A., Ferreira-Dias, S., Miranda, I., & Pereira, H. (2020). Chemical Composition of Cuticular Waxes and Pigments and Morphology of Leaves of *Quercus suber* Trees of Different Provenance. *Plants, 9*(9), 1165. doi:10.3390/plants9091165

Sohretoglu, D., & Renda, G. (2020). The polyphenolic profile of Oak (*Quercus*) species: a phytochemical and pharmacological overview. *Phytochemistry Reviews, 19*(6), 1379–1426. doi:10.1007/s11101-020-09707-3

Spellenberg, R., & Bacon, J.R. (1996). Taxonomy and Distribution of a Natural Group of Black Oaks of Mexico (*Quercus*, Section *Lobatae*, Subsection Racemiflorae). *Systematic Botany, 21*(1), 85–99.

Tanase, C., Nicolescu, A., Nisca, A., Stefănescu, R., Babotă, M., Mare, A.D., Ciurea, C.N., & Man, A. (2022). Biological Activity of Bark Extracts from Northern Red Oak (*Quercus rubra* L.): An Antioxidant, Antimicrobial and Enzymatic Inhibitory Evaluation. *Plants, 11*(18), 2357. doi:10.3390/plants11182357

Thomson, P.M., & Mohlenbrock, R.H. (1979). Foliar Trichomes of *Quercus* in the Eastern United States. *Journal of the Arnold Arboretum, 60*(3), 350–366.

Top, S.M., Preston, C.M., Dukes, J.S., & Tharayil, N. (2017). Climate Influences the Content and Chemical Composition of Foliar Tannins in Green and Senesced Tissues of *Quercus rubra*. *Frontiers in Plant Science, 8*, 423. doi: 10.3389/fpls.2017.00423

Tschan, G.F., & Denk, T. (2012). Trichome types, foliar indumentum and epicuticular wax in the Mediterranean gall oaks, *Quercus* subsection *Galliferae* (Fagaceae): implications for taxonomy, ecology and evolution. *Botanical Journal of the Linnean Society, 169*(4), 611–644. doi:10.1111/j.1095-8339.2012.01233.x

Turner, N.C., & Heichel, G.H. (1977). Stomatal Development and Seasonal Changes in Diffusive Resistance of Primary and Regrowth Foliage of Red Oak (*Quercus rubra* L.) and Red Maple (*Acer rubrum* L.). *New Phytologist, 78*(1), 71–81. doi:10.1111/j.1469-8137.1977.tb01544.x

Uzunova, K., Palamarev, E., & Ehrendorfer, F. (1997). Anatomical changes and evolutionary trends in the foliar epidermis of extant and fossil Euro-Mediterranean oaks (Fagaceae). *Plant Systematics and Evolution, 204*(3/4), 141–159.

Uzunova, K., & Palamarev, E. (1993) An Investigation of the Leaf Epidermis of the European (Non-Balkan) Species of the Genus *Quercus*. *Fitologia, 45*, 3–15.

Valencia, S., & Delgado, A. (2003). Los tricomas foliares en la caracterización de un grupo de especies del género *Quercus*, sección (Fagaceae). *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Botánica, 74*(1), 5–15.

Valladares, F., Chico, J.M., Aranda, I., Balaguer, L., Dizengremel, P., Manrique, E. and Dreyer, E. (2002) The Greater Seedling High-Light Tolerance of *Quercus robur* over Fagus sylvatica Is Linked to a Greater Physiological Plasticity. *Trees, 16*, 395–403.

Volin, P. (2001). Analysis of steroidal lipids by gas and liquid chromatography. *Journal of Chromatography A, 935*(1–2), 125–40. doi:10.1016/S0021-9673(01)01089-5

Xavier, S.K., Devkar, R.A., Chaudhary, S., Shreedhara, C.S., & Setty, M.M. (2015). Pharmacognostical standardization and HPTLC Quantification of Gallic acid in Homonoia riparia Lour. *Pharmacognosy Journal, 7*(6), 383–388. doi:10.5530/pj.2015.6.12

Yiotis, C., Manetas, Y., & Psaras, G.K. (2006). Leaf and green stem anatomy of the drought deciduous Mediterranean shrub *Calicome villosa* (Poiret) Link. (Leguminosae). *Flora, 201*(2), 102–107. doi:10.1016/j.flora.2005.04.007

Yücedağ, C., Sanders, J., Musah, M., & Gailing, O. (2019). Stomatal density in *Quercus petraea* and *Q. robur* natural populations in Northern Turkey. *Dendrobiology, 81*, 58–64. doi:10.12657/denbio.081.007

Zhou, Z.K., Wilkinson, H., & Wu, Z.Y. (1995). Taxonomical and evolutionary implications of the leaf anatomy and architecture of *Quercus* L. subgenus *Quercus* from China. *Cathaya, 7*, 1–34.

Стаття надійшла до редакції 18.07.2024.
Стаття прийнята до друку 23.08.2024.

The authors declare that they have no conflict of interest.
Authors' contribution:
Omelkovets T.S. – collection and analysis of literature, annotations, article writing;
Konovalova O.Yu. – research design, summary, correction of the article;
Shcherbakova O.F. – idea, collection and analysis of literature, conclusions, article writing;
Kalista M.S. – article writing and translation in English;
Hurtovenko I.O. – article writing;
Novosad K.V. – article writing.

Email address for corresponding with the authors: *t.omelkovets@kmu.edu.ua*