

Tree Physiology

Eustaquio Gil-Pelegrín
José Javier Peguero-Pina
Domingo Sancho-Knapik *Editors*

Oaks Physiological
Ecology. Exploring
the Functional
Diversity of Genus
Quercus L.

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Tree Physiology

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Chapter 1

Oaks and People: A Long Journey Together

Eustaquio Gil-Peigrín, José Javier Peguero-Pina
and Domingo Sancho-Knapik

Abstract Genus *Quercus* L. has been closely associated to humans throughout the history, with empirical evidences of such relationship before the appearance of *Homo sapiens* strictly speaking. Since then, mankind has obtained different basic resources from oaks, from acorns as food, charcoal for metal melting or wood as key material for different works. Such relation has been especially strong in some areas where oaks are considered as “tree of life” or “people’s species”. Moreover, the interest of scientists in the study of this genus has provided a lot of new discovers in different areas of the so-called plant sciences. Genus *Quercus*, comprising more than 400 species found throughout the Northern Hemisphere in a lot of contrasted habitats, have been the case study in many papers about taxonomy, palaeobotany, plant physiology or basic and applied ecology. This fact is summarized in this chapter, serving as a preface to this book.

Mankind has established a close relationship with oaks, which are deeply rooted in the folklore, mythology or even religion of many human cultures (Ciesla 2002; Chassé 2016; Out 2017). In fact, Goren-Inbar et al. (2000) recovered *Quercus* sp. rests among the “edible species” found in the Acheulean (Middle Pleistocene, 780,000 years ago) archaeological site of Gesher Benot Ya’aqov (Israel). In a later study, Goren-Inbar et al. (2002) went beyond and suggested that hominins population that occupied this site during this period consumed acorns from *Q. californica* and *Q. ithaburensis*. So, this evidence dates such relationship between oaks and “human” transcends our existence as *Homo sapiens*.

The practise of acorn eating by human hunter-gatherer cultures has been well documented by archaeologists since the Palaeolithic (Cacho 1986; Chassé 2016). Many other archaeological evidences seem to indicate the importance of acorns eating for the survival of pre-Neolithic cultures of the eastern Mediterranean Basin

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(Natufian), living under a Mediterranean-type climate with associated oak woodlands (e.g. McCorrison 1994; Olszewski 2004). This dietary resource remained very important for sedentary cultures, as evidenced by many archaeological sites corresponding to Pre-Roman cultures of the Iberian Peninsula (Pereira-Sieso and García-Gómez 2002). Moreover, the consumption of acorns by people during famine moments, associated to poor harvests, is reported until the 18th century (García-Gómez et al. 2002).

A well-known example of ancestral dependence on the resources offered by oaks is given also by the native cultures of southeastern USA (Fagan 2004). Anderson (2007) used the expression “bread of life” for acorns, due to their paramount importance for the indigenous diet of this region. However, this author went further when defined such relationship, since he also proposed the expression “tree of life” for oaks in their relation with these cultures due to the many other benefits they obtained from these trees. In the same direction, Long et al. (2016) proposed to consider *Q. kelloggii* as a “cultural keystone” species for the indigenous cultures of California and Oregon, in the sense that Garibaldi and Turner (2004) gave to this concept. These indigenous managed traditionally oak forests (Anderson 2005), even with the use of fire to control the dominance of conifers (Ciesla 2002; Anderson 2007), yielding a mutual benefit for humans and oaks, as part of their “traditional ecological knowledge” (Long et al. 2016).

The use nowadays of different resources offered by *Quercus* species to the inhabitants in the “Middle Hills” of Central Himalaya (Shrestha et al. 2013) is another example of the complex dependence between oak woodlands and humans. The many resources that people obtains from these forest communities are so extent that Singh and Singh (1986) used the term “people’s species” for oaks living in this region, with a very special mention to the banj oak (*Q. leucotrichophora*). As is indicated by these authors, the oak woodlands in Central Himalaya offer different benefits for humans, such as forage for cattle, firewood, or compost from leaves to manure the crop fields. Moreover, at a landscape scale, the existence of oaks is clearly related to the amount and quality of spring water, besides the critical influence on soil conservation in a territory of high slopes. However, this complex relationship is fragile and the sustainability is dependent on the exploitation intensity. Shrestha et al. (2013) analysed the coexistence of oaks and humans in Nepal, with especial reference to the situation of *Q. semecarpifolia* stands. They indicated that, while the presence of humans in these “Middle Hills” of the Central Himalaya goes back several millennia, a severe increase in the Nepal population (due to growth and migration) during the last century has dealt to a sobreexploitation of these habitats, with negative effects on forest structure, regeneration and species diversity associated to these ecosystems (Christensen and Heilmann-Clausen 2009). The existence of a high disturbance due to human pressure on these forests has been also pointed out in other areas of the Central Himalaya, severely reducing the viability and the area of banj oak forests (Singh et al. 2014).

In the Iberian Peninsula, a particular exploitation regime of the mediterranean woodlands is the development of cleared oak forests or savannah-like woodlands of *Quercus ilex* subsp. *rotundifolia* or *Q. suber*, constituting the so-called “dehesas” in

Spain or “montados” in Portugal (Rodríguez-Estevez et al. 2012). This agrosilvopastoral system, as considered in Olea and San Miguel-Ayanz (2006), allows humans to obtain different resources from this anthropogenic habitat since the Neolithic (López-Sáez et al. 2007). The maintenance of a traditional extensive pig farming based on an autochthonous porcine breed foraging acorns during the “montanera” is one of the most important benefits obtained from these woodlands (Rodríguez-Estévez et al. 2009). The consumption of acorns has a positive influence on the lipid profile of the carcasses (Cava et al. 1997), which confers a high quality and value-added to those pork products obtained and, hence, to the “dehesa” (Gaspar et al. 2007). However, this agrosilvopastoral system is threatened by severe processes of oak decline, severely affecting the oak stands since the beginning of the 1980s (Gil-Pelegrín et al. 2008). This particular oak decline process, frequently called “seca”, has a proven biological component, with the fungal species *Phytophthora cinnamomi* Rands. as the recognised agent since the very first studies (Brasier et al. 1993; Tuset et al. 1996). To date the concern is maintained, as death of holm and cork oaks persists until now (Avila et al. 2016).

Obviously, oaks have been a source of wood for millennia, and evidences of that are found in different archaeological sites (e.g. De’Athe et al. 2013; Out 2017; Ruiz-Alonso et al. 2017). In some areas, as northern Spain, different studies indicate a continuous use of deciduous *Quercus* species as firewood during several millennia, from the early Neolithic to the early Bronze Age (Ruiz-Alonso et al. 2017). Other archaeological sites allow interpreting the wood of *Quercus* species in a burial context, giving a symbolic value to this genus in many areas of Europe during the Neolithic and subsequent ages (Out 2017). The study of Iron-Age sites in the United Kingdom suggested that humans established a management of oak stands to obtain a regular source of woodland for metalworking (De’Athe et al. 2013). This management is based on the high capability of *Quercus* species for resprouting after cutting (Giovannini et al. 1992), with the production of many small stems in short rotation cycles, which length depends on the species and environmental conditions (Corcuera et al. 2006). This practise, known as coppicing, has been regularly used over time (Barberó et al. 1990), to the extent that this coppice stands are the most common structure in oak woodlands of southern Europe (Serrada et al. 1992; Amorini et al. 1996; Montes et al. 2004). As stated by Cañellas et al. (1994), the traditional practice of coppicing has been reduced since the middle of the 20th century in many areas of Spain, due to important sociological changes that implied a drastic reduction in the demand of firewood or charcoal. This fact leads to the existence of many overaged coppice stands of different *Quercus* species with a reduced growth (Cañellas et al. 1996). Moreover, Corcuera et al. (2006) found that this reduced growth has a negative effect on the hydraulic conductivity of the stems together with a higher vulnerability to water stress during the summer drought period. A progressive transformation of these oak coppices into high forest by thinning may have positive effects on tree growth and soil water availability (Fedorová et al. 2016) or even a greater tolerance to droughts (Rodríguez-Calcerrada et al. 2011).

Oak wood have been also a basic resource through the history as key material for naval construction (e.g. Giachi et al. 2017). It has been documented a massive demand for timber as raw material for the respective fleets during the Modern Age (mainly during the 15th and 16th centuries) in Portugal (Reboredo and Pais 2014) and Spain (Wing 2012), which gave a strategic importance to the oak woodlands there. Furthermore, the use of oak barrel in winemaking is a crucial practice to ensure a high quality of the final product, as oak wood adds different compounds that contribute to improve the wine flavour and colour (e.g. Chira and Teissedre 2013). In this sense, the so-called “American oak” (*Quercus alba*), the “French oak” (*Q. robur* and *Q. petraea*) and *Q. pyrenaica* (Jordão et al. 2006) are the most common species for barrel cooperage, with a differential influence on wine characteristics (see Chira and Teissedre 2015). Additionally, a bottle of good wine is corked with a very particular product obtained also from the bark of a very concrete *Quercus* species. Effectively, the properly called cork oak (*Q. suber*) has traditionally provided the key material for that purpose, indicating that oaks play an outstanding role in the process of wine-making.

Another important contribution of oaks to the economy in many areas of southern Europe (Italy, France and Spain) and Australia are the production of edible fungi of very high added value and internationally related to the haute cuisine (Reyna and García-Barreda 2014) We are particularly referring to the hypogeous fruiting body of different species of the genus *Tuber*, the so-called truffles, in mycorrhizal symbiosis with different *Quercus* species, with *Q. ilex* as the most common host. As stated by Aumeeruddy-Thomas et al. (2012), gathering these mushrooms is a recognised and documented activity in France since the Middle Age. Concerning *Tuber melanosporum*, one of the “quintessential truffle” (Reyna and García-Barreda 2014), it can be artificially produced in planted truffle orchards since the 19th century (Olivier et al. 1996) in many areas under Mediterranean-type climates. In Spain, truffle production has been a new opportunity in areas suffering from severe problems of depopulation (e.g. the province of Teruel), which adds a social value to truffle and to the *Quercus* species, without which this cultivation would not be possible.

Thus, genus *Quercus* has been culturally and economically linked to humans since millennia. But, otherwise, oaks have been food for thought in plant sciences as this book reflects. *Quercus* L. (*Fagaceae*) has an outstanding role in the vegetation of the Northern Hemisphere and can be considered the most diverse Northern Temperate tree genus. It comprises ca. 400 tree and shrub species distributed among contrasting phytoclimates, from temperate and subtropical forests to mediterranean evergreen woodlands (Manos et al. 1999; Kremer et al. 2012). More specifically, oaks live in a great variety of environments, from subalpine forests (e.g. the Alborz Mountains in northern Iran) to semiarid forests (Afghanistan, the Mediterranean region and western North America) and riparian and swamp forests in different parts of the world (for example wetlands of Florida, Alabama, or the riparian forests of the Danube river), even touching the Tropics in SE Asia and Central South America. Exploring this complexity is an opportunity and also a challenge for naturalists.

This wide geographical range and phytoclimatic diversity has a direct expression in terms of taxonomic complexity. A considerable number of studies about phylogeny of oaks have been carried out in order to get an overview about this large modern diversity of oaks (see Chap. 2 for a comprehensive review). Up to now, all of the successive infrageneric classifications of *Quercus* have recognized the same major groups (see Denk and Grimm 2010 and references therein). In Chap. 2 of this book, Denk et al. propose a revised classification of *Quercus* based on pollen morphology that includes two subgenera, *Quercus* and *Cerris*. On the one hand, subgenus *Quercus* comprises 5 sections: section *Ponticae*, section *Virentes*, section *Protobalanus*, section *Quercus*, and section *Lobatae*. On the other hand, subgenus *Cerris* comprises 3 sections: section *Cerris*, section *Ilex*, and section *Cyclobalanopsis*. Subgenus *Cerris* is confined to the Old World, while subgenus *Quercus* is distributed throughout Northern Hemisphere.

Genus *Quercus* is an ancient lineage of *Fagaceae* whose first records are pollen grains of the late Paleocene age, as described in Chap. 3 by Barrón et al. Since the Eocene, oaks diversified and spread throughout the Northern Hemisphere. As today, they inhabited very different environments, both temperate and cold-temperate regions (suggesting an unequivocal Arctotertiary origin) or tropical and subtropical realms (indicating a Palaeotropical origin). However, one particular group of fossil *Quercus* species, those belonging to section *Cyclobalanopsis* (sensu Denk et al. in Chap. 2 of this book and formerly subgenus *Cyclobalanopsis*), always shows a tropical-subtropical distribution, being common on the Palaeotropical Tethyan shores of North America and Eurasia during great part of the Cenozoic. The analysis of the information given by the palaeontological records in contrast with the present distribution and ecology of closely related species may serve for a good reconstruction of the palaeoecology of the Northern Hemisphere since the Cenozoic.

The ecological importance and functional diversity of genus *Quercus* has been also addressed in many ecophysiological studies concerning the response of different oak species to several abiotic stress factors. Chapter 4, by Cavender-Bares and Ramírez-Valiente, explores the adaptative response of an interesting study case in a particular lineage of American oaks, namely the live oaks (*Quercus* section *Virentes* Nixon), with species such as *Quercus virginiana*, *Q. geminata*, *Q. fusiformis* or *Q. oleoides*. Several of these live oaks span the Tropical-Temperate divide (Koehler et al. 2012), which implies the existence of different conditions of water availability besides different temperature registers during winter, including freezing values. These authors offer new insights about the existence of local adaptative responses within species in terms of withstanding both drought and freezing. Moreover, they also report interspecific differences in this set of closely phylogenetically related species with similar physiognomic features.

The existence of a drought period during summer, due to the combination of a temperature monthly maximum and a precipitation minimum is the most distinctive characteristic of the Mediterranean-type climates. Chapter 5, by Gil-Pelegrín et al., delves into the ecophysiological features of the many *Quercus* species inhabiting areas under this particular climate, as compared with oaks from areas with

Temperate, wet Tropical and dry Tropical climates. In this chapter, two very different mediterranean oaks are recognised and compared: (i) evergreen and sclerophyllous species (e.g. *Quercus ilex*) and (ii) malacophyllous or semi-sclerophyllous winter deciduous oaks (e.g. *Quercus faginea*). The coexistence of these two leaf habits in mediterranean oaks seems to be the consequence of different paleogeographical origins, with winter-deciduous (from an Arctotertiary geoflora) and evergreen (from the Palaeotropical geoflora) co-occurring in a complex patchwork. In most mediterranean areas, the balance has tipped in favor of evergreen species (such as *Quercus ilex* subsp. *rotundifolia*) through the ancestral alteration of the soil by humans, as these species with a longer leaf life span seem to better response to the splitted vegetative period induced by summer drought and winter cold. The leaf life span in *Quercus* species under mediterranean-type climates is the central aim of Chap. 6, where Escudero et al. state that the most striking difference among *Quercus* species inhabiting these areas is the dichotomy represented by the deciduous and evergreen habits, which major implications in terms of leaf anatomy, carbon gain, cost construction and maintenance.

Quercus L. has been proposed as an outstanding genus to understand how hybridation and introgression influence the evolution of plants. Thus, in Chap. 7, López de Heredia et al. revised several evidences of ancient introgressions between two mediterranean evergreen oaks, namely *Q. ilex* and *Q. suber*, and update estimations of present hybridation rates. These authors concluded that these processes seem to be a very relevant mechanism explaining some distribution and ecological patterns of these species, especially during glaciations.

Concerning the hydraulic conductivity of the xylem, genus *Quercus* has been the object of many studies since the very first steps in the study of this key topic in tree functioning, both from anatomical and biophysical or physiological points of view. Some of the seminal ideas proposed by Zimmermann (1983), such as the architecture of the water-conduction pathway of a tree or the segmentation hypothesis were early explored in species of *Quercus* (e.g. Cochard and Tyree 1990; Lo Gullo and Salleo 1993). In Chap. 8, Robert et al. explore the bibliography concerning the xylem anatomy in oak species, focussing on the overall variation in the xylem structural and functional features, with special incidence on the different performance of the ring-porous (with few wide vessels) and diffuse-porous wood (with numerous narrow vessels) within this genus.

Oaks have also been subject of study in several processes related to CO₂ assimilation (mesophyll conductance and photosynthesis in Chap. 9) and loss (respiration and volatile organic compounds emission in Chap. 10). Moreover, it should be noted that oaks are main targets in seminal papers concerning the implementation of new methodologies and techniques for the estimation of mesophyll conductance. Thus, the method based on the simultaneous measurement of gas exchange and chlorophyll fluorescence parameters was firstly used in *Q. ilex* (Di Marco et al. 1990) and *Q. rubra* (Harley et al. 1992). This method was firstly compared with the stable carbon isotope fractionation technique (Evans et al. 1986) for both species by Loreto et al. (1992). More recently, the validation of mesophyll conductance modelled on the basis of anatomical characteristics has been carried

out in several deciduous and evergreen oak species (Tomás et al. 2013; Peguero-Pina et al. 2016, 2017). These studies in different *Quercus* species have reinforced the prevailing role of leaf anatomy in mesophyll conductance and net CO₂ assimilation, as stated by Peguero-Pina et al. in Chap. 9. Oaks also constitute an excellent taxonomic group to study the variability in carbon losses from respiration and the emission of volatile organic compounds among different plant functional types and environmental conditions (see Chap. 10 by Salomón et al.). These authors conclude that, besides carbon assimilation, it would be necessary a comprehensive understanding of carbon loss in oaks to accurately assess carbon cycling in current and future scenarios of climate change. In other cases, some physiological mechanisms have also been firstly showed in *Quercus* species, such as some photo protective mechanisms stated in Chap. 11 by García-Plazaola et al. Thus, a xanthophyll cycle involving the so-called “lutein epoxide cycle” was described for the first time in non-parasitic woody plants by García-Plazaola et al. (2002) in eight oak species. In line with this, Peguero-Pina et al. (2009) found that *Q. ilex* and *Q. coccifera* showed a drought-mediated chronic photoinhibition and an overnight retention of de-epoxidated forms of xanthophyll cycle (i.e. anteraxanthin and zeaxanthin).

Villar et al., in Chap. 12, show how long *Quercus* provides an interesting study case for analysing the traits involved in growth processes, due to the high variability of functional traits there found, following the postulates of the leaf economics spectrum. In this chapter, it is evidenced that seedlings of *Quercus* species were characterized, among other traits, by a low relative growth rate (RGR) and a high root mass ratio (RMR), while leaf dry mass per area ratio (LMA) explains most of the differences in RGR among oak species. Moreover, the proportion of biomass in leaves and roots decreased with tree size, by contrast increasing the biomass in stems. According to this, bigger trees grow more slowly. In spite of this, the authors conclude that seedling RGR under controlled conditions is positively related with that of adult trees in the field. Such conclusion offers a way for comparative studies at a wide scale.

Chapter 13, by Rodríguez-Calcerrada et al., evidences how much oaks have been threatened in many areas of the world, trough massive oak decline processes which have affected species belonging to clearly separate taxonomic groups, with different leaf habit and/or physiological performance. This fact has promoted the concern of foresters and scientific community about the different oak decline processes reported in Central Europe and Northeastern USA since the 18th and 19th centuries (Millers et al. 1989; Thomas 2008). Since then and up to now, more episodes of oak decline were reported over a wide range of sites in most forested places of the northern hemisphere, including deciduous and evergreen species, as described in Chap. 13 by Rodríguez-Calcerrada et al. These authors note that most oak decline episodes have been observed after extreme climatic events (severe droughts, waterlogging or after consecutive events of winter freezing), but they have also been associated to different pathogens and site conditions. In most cases, the interaction of at least two stress agents, where one of them is often an extreme climatic event, has triggered important outbreaks of decline.

In order to preserve the oak woodlands from vanishing, if these massive decline processes become more frequent, the improvement of new seedling recruitment may be a challenge to be solved. In genus *Quercus*, the inherent biological limitations to the natural regeneration of oaks, and especially in a degraded landscape by human intervention, makes their natural expansion quite difficult. For this reason, it is necessary the implementation of techniques to facilitate this process in an artificial way (as is reviewed in Chap. 14 by Pemán et al.), from cultivation methods in the nursery phase to the final installation in the field.

This book also highlights the overall importance of oaks from an ecological viewpoint (see Chap. 15 by Madrigal-González et al.). Madrigal-González et al. state that oak forests are highly valued ecosystems from the viewpoint of human economical and cultural interests, and their distribution and physiognomy has been greatly modulated by humans since the Neolithic (Barbero et al. 1990). Madrigal-González et al. in Chap. 15 also conclude that, not only climatic fluctuations, but also agricultural intensification and, more recently, widespread agricultural land abandonment associated with human migration from rural to urban areas are recognized as major forces leading to recent oak encroachment, expansion or decline in different European regions.

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Chapter 2

An Updated Infrageneric Classification of the Oaks: Review of Previous Taxonomic Schemes and Synthesis of Evolutionary Patterns

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Abstract In this chapter, we review major classification schemes proposed for oaks by John Claudius Loudon, Anders Sandøe Ørsted, William Trelease, Otto Karl Anton Schwarz, Aimée Antoinette Camus, Yuri Leonárdovich Menitsky, and Kevin C. Nixon. Classifications of oaks (Fig. 2.1) have thus far been based entirely on morphological characters. They differed profoundly from each other because each taxonomist gave a different weight to distinguishing characters; often characters that are homoplastic in oaks. With the advent of molecular phylogenetics our view has considerably changed. One of the most profound changes has been the realisation that the traditional split between the East Asian subtropical to tropical subgenus *Cyclobalanopsis* and the subgenus *Quercus* that includes all other oaks is artificial. The traditional concept has been replaced by that of two major clades, each comprising three infrageneric groups: a Palearctic-Indomalayan clade including Group Ilex (Ilex oaks), Group Cerris (Cerris oaks) and Group Cyclobalanopsis (cycle-cup oaks), and a predominantly Nearctic clade including Group Protobalanus (intermediate or golden cup oaks), Group Lobatae (red oaks) and Group Quercus (white oaks,

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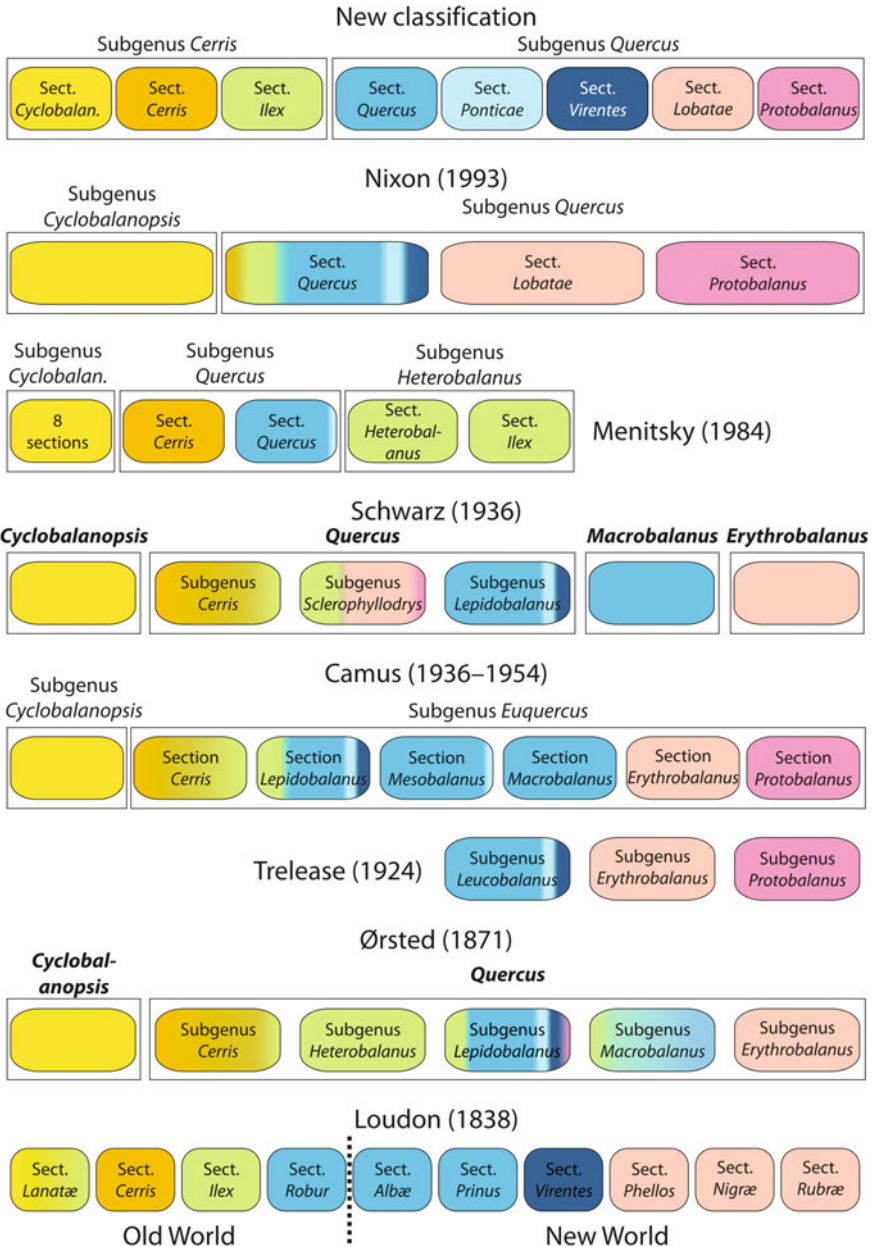
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Fig. 2.1 Classification schemes for *Quercus* from Loudon to Nixon. Colour coding denotes the actual systematic affiliation of species included in each taxon: of the ‘Old World’ or ‘mid-latitude clade’ section *Cyclobalanopsis* (cycle-cup oaks, yellow), section *Cerris* (Cerris oaks; orange), and section *Ilex* (Ilex oaks; green); and of the ‘New World’ or ‘high-latitude clade’ section *Quercus* (white oaks s.str.; blue), sections *Virentes* (cyan) and *Ponticae* (dark blue), section *Protobalanus* (intermediate oaks; purple), and section *Lobatae* (red oaks; red). Colour gradients are proportional, i.e. reflect the proportion of species with different systematic affiliation included in each taxon. Names in bold were treated as genera. Note: Menitsky (1984) and Trelease (1924) only treated the Eurasian and American oaks, respectively, and provided classifications in (nearly) full agreement with current phylogenies

with most species in America and some 30 species in Eurasia). In addition, recent phylogenetic studies identified two distinct clades within a wider group of white oaks: the *Virentes* oaks of North America and a clade with two disjunct endemic species in western Eurasia and western North America, *Quercus pontica* and *Q. sadleriana*. The main morphological feature characterising these phylogenetic lineages is pollen morphology, a character overlooked in traditional classifications. This realisation, along with the now available (molecular-)phylogenetic framework, opens new avenues for biogeographic, ecological and evolutionary studies and a re-appraisal of the fossil record. We provide an overview about recent advances in these fields and outline how the results of these studies contribute to the establishment of a unifying systematic scheme of oaks. Ultimately, we propose an updated classification of *Quercus* recognising two subgenera with eight sections. This classification considers morphological traits, molecular-phylogenetic relationships, and the evolutionary history of one of the most important temperate woody plant genera.

2.1 History of Classifications of Oaks

In his original work, Carl von Linné listed 14 species of oaks from Europe and North America: the white oaks *Q. alba*, *Q. æsculus* (= *Q. petraea* (Matt.) Liebl.), *Q. robur*, and *Q. prinus* (status unresolved); the red oaks *Q. rubra*, *Q. nigra*, and *Q. phellos*; the Cerris oaks *Q. cerris*, *Q. ægilops* (= *Q. macrolepis* Kotschy), *Q. suber*; and the Ilex oaks *Q. ilex*, *Q. coccifera*, *Q. gramuntia* (= *Q. ilex*), and *Q. smilax* (= *Q. ilex*) (Linné 1753). This number had increased to 150 species when Loudon (1838, 1839) provided the first infrageneric classification of oaks recognising ten sections based on reproductive and leaf characters. Eight of Loudon’s sections (*Albæ*, *Prinus*, *Robur*; *Nigræ*, *Phellos*, *Rubræ*; *Cerris*; *Ilex*) were based on species described by Linné (Fig. 2.1). New additions were the (fully) evergreen south-eastern North American “Live Oaks”, sect. *Virentes*; and the “Woolly-leaved Oaks”, sect. *Lanatae*, of Nepal (including an Ilex oak and a species that was later recognised as a cycle-cup oak). Loudon’s classification is remarkable in one aspect: he established the fundamental subdivision of European oaks (his sections *Cerris*, *Ilex*, and *Robur*). This subdivision, although modified, occurs in nearly all later classifications and corresponds to clades in most recent molecular-phylogenetic



trees (cerroid, ilicoid, and roburoid oaks; cf. Denk and Grimm 2010; A. Hipp and co-workers, work in progress).

Ørsted (1871) can be credited for recognising an important Asian group of oaks hardly known at the time of Loudon and originally associated with *Cyclobalanus*

(= *Lithocarpus*): the cycle-cup oaks of subtropical and tropical East Asia, which Ørsted considered distinct from *Quercus* as genus *Cyclobalanopsis*, within his subtribe Quercinae (Fig. 2.1). This concept was adopted by later researchers (e.g. Camus 1936–1938; Nixon 1993; as subgenera) and is still used for the Flora of China (Huang et al. 1999; Flora of China 2016). Within the second genus of the Quercinae, *Quercus*, Ørsted recognised five subgenera with a total of 16 sections and about 184 species. His work is the first to treat oaks in a global context; Loudon, and later Camus, Trelease, and Menitsky, treated the Nearctic and Palearctic-Indomalayan taxa independently.

In the early 20th century, two competing classification concepts emerged, which were henceforth used by researchers (partly until today). The central/eastern European tradition followed in principle the classification system of Schwarz (1936), whereas the western/southern European tradition relied on the monographic work of Camus (1936–1938, 1938–1939, 1952–1954). A decade earlier, Trelease (1924) provided a comprehensive treatment of the American oaks listing about 371 species (nearly half of them new) in 138 series and three subgenera/sections (Fig. 2.1): *Leucobalanus* (white oaks), *Erythrobalanus* (red oaks), and *Protobalanus* (intermediate oaks). Thus, he established the tripartition of the genus in the Americas (sections *Quercus*, *Lobatae*, *Protobalanus*; (Jensen 1997; Manos 1997; Nixon and Muller 1997). Camus and Schwarz (partly) followed Trelease regarding the classification of the American oaks, but disagreed with respect to the oaks of Eurasia and North Africa, specifically on how to classify the American oaks in relation to their Eurasian counterparts. Camus followed Ørsted's general scheme, but recognised a single genus *Quercus* with the two subgenera *Cyclobalanopsis* and *Quercus*. She downgraded Ørsted's subgenera in *Quercus* to sections (Fig. 2.1). Schwarz (1936) also followed in principle the concepts of Ørsted, but raised Ørsted's categories, erecting a two tribe system (Cyclobalanopsidae, Querceae) with two genera each (*Cyclobalanopsis* + *Erythrobalanus*, *Macrobalanus* + *Quercus*). A novelty in the system of Schwarz was the subgenus *Sclerophyllodrys* (Fig. 2.1), in which he accommodated many sclerophyllous oaks of Eurasia, Trelease's subgenus *Protobalanus* (including an Asian series *Spathulatae*), and six evergreen series of Trelease's subgenus *Erythrobalanus*. Another major difference relative to Camus was that Schwarz adopted Ørsted's global concept by grouping North American and Eurasian white oaks in the same sections (*Dascia*, *Gallifera*, *Prinus*, *Roburoides*).

The most recent monographic work towards a new classification of oaks was the one of Menitsky (1984, translated into English in 2005) dealing with Asian oaks (Fig. 2.1). Except for a single species (*Q. suber*), Menitsky placed all Ilex oaks in subgenus *Heterobalanus*, while Cerris oaks (except for *Q. suber*) formed one of the two sections in subgenus *Quercus* (the other section included the white oaks). Menitsky's account is the only morphology-based system that correctly identified the natural groups of Eurasian oaks confirmed later by palynological and molecular data. In the same way, Trelease's sections of American oaks also have been confirmed as natural groups.

The latest and currently most widely used (e.g. Govaerts and Frodin 1998; see also www.wikipedia.org and www.internationaloaksociety.org) classification is by

Nixon (1993), published as a review. Nixon adopted the concept of Camus but merged her sections *Cerris*, which comprised *Cerris* and *Ilex* oaks, and *Euquercus*, comprising the remaining *Ilex* oaks and the white oaks, into a single section *Quercus*. According to this latest modification of Ørsted's more than 150 years old scheme, the genus *Quercus* is divided into two subgenera, the cycle-cup oaks (*Cyclobalanopsis*) and all remaining oaks (*Quercus*). Subgenus *Quercus* includes two natural sections, one comprising the red oaks (sect. *Lobatae*) and one comprising the intermediate oaks (sect. *Protobalanus*), and a heterogeneous, artificial, northern hemispheric section *Quercus* including all white oaks, *Cerris* and *Ilex* oaks (Fig. 2.1).

2.2 Change in Criteria for Classification

There are two major causes for the differences in the traditional, morphology-based classifications of oaks: (1) the weighing of morphological characters, (2) the geographic regions considered. Convergent morphological evolution is a common phenomenon in the genus *Quercus* and the Fagaceae in general (Oh and Manos 2008; Kremer et al. 2012). For instance, Loudon's (1838) descriptions for the distantly related sections *Ilex* (Eurasian *Q. ilex* and relatives) and *Virentes* (North American *Q. virens* Ait. [= *Q. virginiana* Miller], a white oak relative) are essentially identical. For similar reasons, Ørsted (1871) included a section *Ilex* in his subgenus *Lepidobalanus* (white oaks in a broad sense), while expanding this section to include evergreen North American white oaks (the sect./subsect. *Virentes* of Loudon, Trelease, Camus, etc.) On the other hand, the Himalayan *Ilex* oak *Q. lanata* was included in Ørsted's section *Prinus* of North American white oaks. The assumption that leaf texture can be used to assign species to higher taxonomic groups on a global scale supports Schwarz' largely artificial subgenera (and genera to some degree). Using the descriptions by Trelease, the Eurasian *Ilex* oaks would still fall in his subgenus *Protobalanus*, and the same is true for the descriptions in Nixon (1993) and the Flora of North America (Manos 1997).

Nixon's concept of a section *Quercus* including all white, *Cerris* and *Ilex* oaks primarily relies on the basal position of aborted ovules in these groups. Much earlier, de Candolle (1862b) noted this feature as being variable in different oak species, and Camus (1936–1938, p. 40f) emphasised that this trait is stable not only within a species, but also characterises groups of species (but see general descriptions in Menitsky 1984). Nixon also adopted Camus' concept of subgenus *Cyclobalanopsis* (aborted ovules always apical; but see general description provided by Huang et al. 1999). Apical abortive ovules are also found in most but not all subsections of sect. *Erythrobalanus* (the red oaks) and in the castanoid genera. Therefore, Nixon suggested that basal abortive ovules are a synapomorphy of his sect. *Quercus*. Subsequent work has shown that the position of aborted ovules in the mature seeds of *Quercus* is the result of different developmental processes and less

Table 2.1 Different contributions of placenta and funiculus to the position of aborted ovules in mature seeds of *Quercus*

Section	<i>Quercus Ponticae Virentes</i>	<i>Lobatae</i>	<i>Protobalanus</i>	<i>Cyclobalanopsis</i>	<i>Cerris</i>	<i>Ilex</i>
Position of aborted ovules	Basal	Apical Type I	Apical, basal, or lateral	Apical Types I, III	Apical, basal or lateral Type II	Basal or lateral Types II, III
Placenta	Sessile	Elongated	?	Elongated	Sessile (compressed)	Sessile or elongated
Funiculus	Sessile	Sessile	?	Sessile or elongated	Sessile or elongated	Sessile or elongated

Type I: apical/lateral aborted ovules by elongated placenta, **Type II:** by elongated funiculus, **Type III:** both elongated placenta and funiculus. Other Fagaceae (*Castanea*, *Castanopsis*, *Lithocarpus*, *Trigonobalanus*) have Types I & III aborted ovules. All other Fagaceae have apical aborted ovules. Information compiled from Borgardt and Pigg (1999), Borgardt and Nixon (2003), Deng (2007), Deng et al. (2008), and Min Deng, unpublished data

stable than originally assumed (Borgardt and Pigg 1999; Borgardt and Nixon 2003; Deng et al. 2008) (Table 2.1).

The only two classification schemes that recognised the same groups later recovered in molecular studies are those by Trelease (1924) and Menitsky (1984). Notably, these monographs were restricted to American and Eurasian oaks, respectively. Therefore, they did not run the risk of creating artificial groups including morphologically similar but unrelated Old World and New World species.

2.3 Changing from Morphology to Molecules

The first molecular phylogeny of *Quercus* including a comprehensive oak sample is the one of Manos et al. (2001) based on sequences of the nuclear ITS region and plastid RFLP data. While Manos et al.'s molecular phylogeny included only a limited sample of Old World species, it challenged the traditional views of Ørsted until Nixon. Instead, the intermediate and white oaks grouped with the red oaks, forming the 'New World Clade', but not with the *Cerris* and *Ilex* oaks. The latter formed an 'Old World Clade' that later would be shown to include the cycle-cup oaks (Manos et al. 2008). While the red oaks and cycle-cup oaks were resolved in well-supported and distinct clades within their respective subtrees, the situation appeared more complex for Camus' section *Cerris* (including a few *Ilex* oaks) and the white oaks (Manos et al. 2001). The lack of unambiguous support may be one reason, why morphologists and oak systematists did not readily implement the new

evidence (e.g. Borgardt and Nixon 2003; le Hardÿ de Beaulieu and Lamant 2010; see also www.internationaloaksociety.org). The other reason is probably that the two new clades lacked compelling, unifying morphological traits.

Plastid gene regions commonly used in plant phylogenetics turned out to be less useful for inferring infrageneric and inter- to intraspecific relationships in oaks. This is mainly because the plastid genealogy is largely decoupled from taxonomy and substantially affected by geography (e.g. Neophytou et al. 2010, 2011; Simeone et al. 2016; Pham et al. 2017). Using genus- to family-level plastid data sets, even when combined with nuclear data, oaks are consistently recognised as a diphyletic group. This is best illustrated in Manos et al. (2008): one moderately supported main clade comprises the ‘New World Clade’ of oaks and *Notholithocarpus*, a monotypic Fagaceae genus of western North America; the other major clade comprises the Eurasian Fagaceae *Castanea* and *Castanopsis*, and the ‘Old World Clade’ of *Quercus*. The phenomenon is also seen in broadly sampled plastid data sets and can produce highly artificial molecular phylogenies (e.g. Xiang et al. 2014; Xing et al. 2014) as discussed in Grímsson et al. (2016). Nevertheless, all currently available plastid data reject the traditional subdivision into two subgenera *Cyclobalanopsis* and *Quercus*: the overall signal (e.g. Manos et al. 2008) is in line with the ‘New World/Old World Clade’ concept introduced by Oh and Manos (2008).

In view of the problems encountered with plastid sequence data, oak molecular phylogenetics concentrated on nuclear-encoded sequence regions. Nine years after the study by Manos et al. (1999), the first ITS phylogeny was confirmed and supplemented by data from a single-copy nuclear gene region, the *Crabs Claw* (*CRC*) gene (Oh and Manos 2008). Denk and Grimm (2010) provided an updated Fagaceae ITS tree including more than 900 individual sequences of oaks (including c. 600 newly generated for western Eurasian species taking into account substantial intra-individual variation). Their data on the 5S intergenic spacer (over 900 sequences), a multicopy nuclear rDNA gene region not linked with the ITS region, supported three groups of western Eurasian oaks as originally conceived by Menitsky (1984). Hubert et al. (2014) compiled new data from six single-copy nuclear gene regions and combined the new data with ITS consensus sequences (based on Denk and Grimm 2010) and *CRC* sequence data (Oh and Manos 2008). Most recently, Hipp et al. (2015) showed a tree based on a large, nuclear reduced representation next-generation sequencing (RADseq) data set. All these data sets and analyses support the recognition of two, reciprocally monophyletic groups of oaks (Fig. 2.2) that can be formalised as two subgenera with eight phylogenetic lineages (Hubert et al. 2014; Hipp et al. 2015), accepted here as sections that match the morphological groups originally perceived by Trelease (1924) and Menitsky (1984):

- **Subgenus *Quercus***, the ‘New World clade’ (Manos et al. 2001) or ‘high-latitude clade’ (Grímsson et al. 2015; Simeone et al. 2016), including
 - the North American intermediate oaks, **section *Protobalanus*** (= Trelease’s subgenus of the same name);
 - the western Eurasian-western North American disjunct **section *Ponticae***;
 - the American “southern live oaks”, **section *Virentes***;

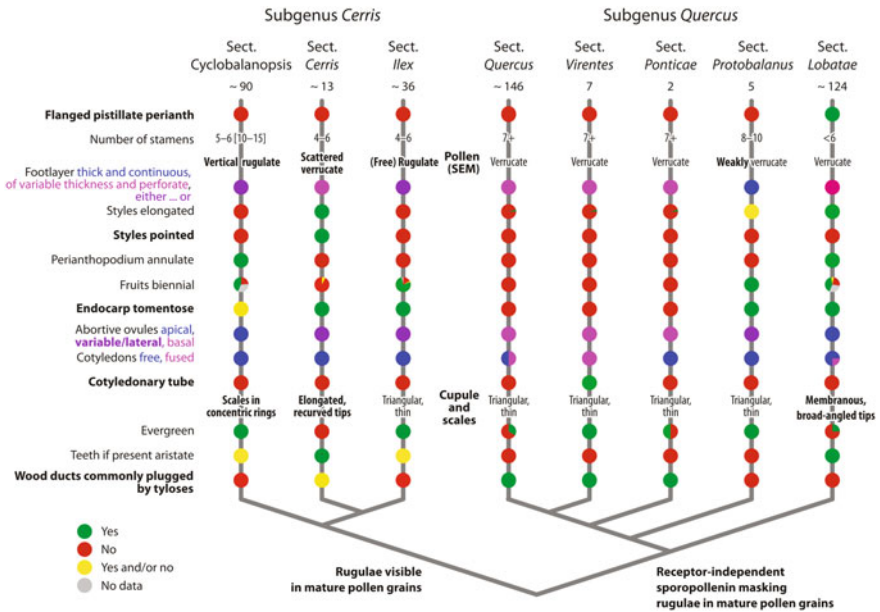


Fig. 2.2 Revised sectional classification of oaks and diagnostic characters of lineages. The basic phylogenetic relationships of the six infrageneric groups of oaks are shown, formalised here as sections in two monophyletic subgenera, subgenus *Cerris* (‘Old World’ or ‘mid-latitude clade’) and subgenus *Quercus* (‘New World’ or ‘high-latitude clade’). **Section-specific traits in bold**; subgenus-diagnostic traits indicated at the respective branches of the schematic phylogenetic tree (Hubert et al. 2014; Hipp et al. 2015). Most traits are shared by more than one section of oaks including non-sister-lineages (normal font); they evolved convergently or are potentially plesiomorphic traits. Some are variable within a section as indicated by (semi-)proportional pie charts. Nonetheless, each section can be diagnosed by unique, unambiguous character suites. Note: ‘yes’ (green) and ‘no’ (red) refers to whether the mentioned trait is observed or not in members of the section, but should not be generally viewed as derived or ancestral

- all white oaks from North America (= Trelease’s subgenus *Leucobalanus*) and Eurasia (= Menitsky’s section *Quercus*), **section *Quercus***; and
- the North American red oaks, **section *Lobatae*** (= Trelease’s subgenus *Erythrobalanus*).
- **Subgenus *Cerris***, the exclusively Eurasian ‘Old World clade’ (or ‘mid-latitude clade’), including
 - the cycle-cup oaks of East Asia (including Malaysia), **section *Cyclobalanopsis*** (former [sub]genus *Cyclobalanopsis* of Ørsted, Camus, Schwarz, Menitsky, and Nixon);
 - the Ilex oaks, **section *Ilex*** (= Menitsky’s subgenus *Heterobalanus* minus *Q. suber*); and
 - the Cerris oaks, **section *Cerris*** (= Menitsky’s section *Cerris* plus *Q. suber*).

2.4 Revised Subgeneric and Sectional Classification of Oaks

The following information for diagnostic morphological characters for the recognised groups of oaks is based mostly on information provided in Trelease (1924), Camus (1936–1938, 1938–1939, 1952–1954), Schwarz (1936, 1937), Menitsky (1984), le Hardy de Beaulieu and Lamant (2010), and the Floras of China (Huang et al. 1999) and North America (Flora of North America Editorial Committee 1997). Information on pollen morphology is from Rowley et al. (1979), Solomon (1983a, b), Rowley and Claugher (1991), Rowley (1996), Rowley and Gabarayeva (2004), Denk and Grimm (2009), Makino et al. (2009), and Denk and Tekleva (2014). Updated information on the position of aborted ovules and the relative contributions of placenta and funiculus to it is from Borgardt and Nixon (2003), Deng et al. (2008), and Min Deng (unpublished data).

If no reference is provided, most monographers (Trelease 1924; Schwarz 1936; Camus 1936–1938; Schwarz 1937; Camus 1938–1939, 1952–1954; Menitsky 1984) agreed on a particular character. Trelease (1924) emphasised the importance of wood characters for delimitation of major groups of American oaks. According to Trelease (1924), Menitsky (1984), and Akkemik and Yaman (2012) the type of wood porosity and presence or absence of tyloses plugging vessels of early-wood are clade-specific to some degree.

Group-specific traits are highlighted by italics (see also Fig. 2.2).

2.4.1 *Genus Quercus*

1753, Sp. Pl., 1: 994.

Lectotype: *Quercus robur* L. (selected by Britton and Brown, Ill. Fl. N. U.S. ed. 2. 1: 616, 7 Jun 1913; confirmed by Green, in Sprague, Nom. Prop. Brit. Bot.: 189, Aug 1929)

Trees 20–30(–55) m high, or **shrubs**; monoecious, evergreen or deciduous; **propagating** from seeds (saplings) or, occasionally, vegetative propagation (ramets); **bark** smooth or deeply furrowed or scaly or papery, corky in some species; **wood** ring-porous or (semi) diffuse-porous, tyloses common in vessels of early-wood or rarely present; **terminal buds** spherical to ovoid, terete or angled, all scales imbricate; **leaves** spirally arranged, stipules deciduous and inconspicuous or sometimes retained until the end of the vegetative period; **lamina** chartaceous or coriaceous, lobed or unlobed, margin entire, dentate or dentate with bristle-like extensions; **primary venation** pinnate; **secondary venation** eucamptodromous, brochidodromous, craspedodromous, semicraspedodromous, or mixed; intersecondary veins present or absent; **inflorescences** unisexual in axils of leaves or bud scales, usually clustered at base of new growth; **staminate inflorescences** lax, racemose to spicate; **pistillate inflorescence** usually stiff, a simple spike, with

terminal cupule and sometimes one to several sessile, lateral cupules; **staminate flowers** subsessile, in dichasial clusters of 1–3(–7) (section *Cyclobalanopsis*) or solitary; subtending bracts persistent or caducous, commonly longer than the perianth, sepals connate to varying degrees forming a shallowly or deeply lobed perianth, stamens (2–)6(–15), anthers short or long, apically notched or apiculate to mucronate, pistillodes reduced and replaced by a tuft of silky hairs; **pollen** monad, medium-sized or small (size categories according Hesse et al. 2009), 3-colp(or)ate, shape prolate, outline in polar view trilobate or rounded, in equatorial view elliptic to oval, tectate, columellate; pollen ornamentation (micro) rugulate, (micro) rugulate-perforate, or (micro) verrucate, (micro)verrucate-perforate; foot layer discontinuous or continuous, of even or uneven thickness; **pistillate flower** one per cupule, with 1–2 subtending bracts, sepals connate, (3–)6(–9) lobed, either situated directly on the tip of the ovary or on the perianthopodium (stylopodium); carpels and styles 3–6, occasionally with staminodes, styles with a broad stigmatic surface on adaxial suture of style (less prominent in section *Cyclobalanopsis*); **ovules** pendent, anatropous or semi-anatropous; **position of aborted ovules** apical, basal, or lateral depending on whether or not the placenta and/or funiculus are secondarily elongated; **fruit** a one-seeded nut (acorn) with a proximal scar, fruit maturation annual or biennial, nut one per cup, round in cross-section, not winged, cotyledons free or fused; **endocarp** glabrous or tomentose; **cup** covering at least base of nut,

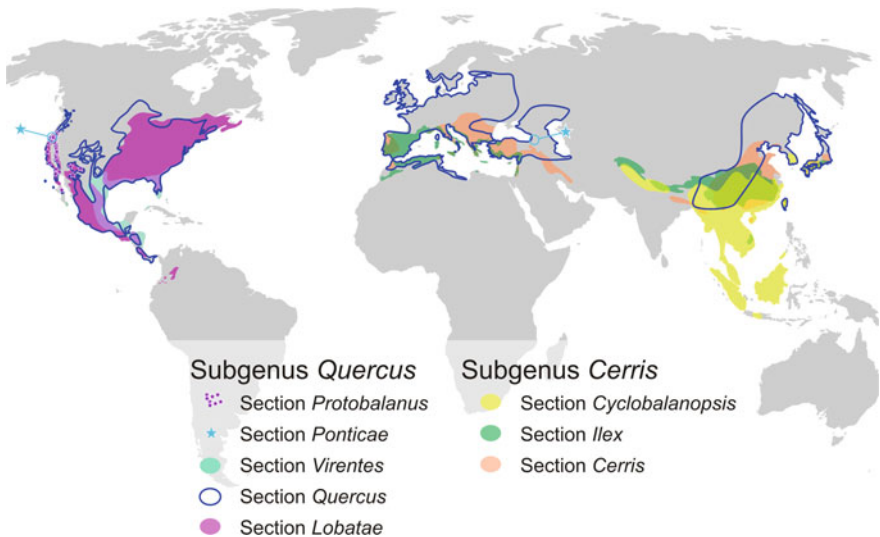


Fig. 2.3 Geographic distribution of the eight sections of *Quercus*. Distribution data from Browicz and Zieliński (1982), Menitsky (1984), Costa Tenorio et al. (2001), Deng (2007), Fang et al. (2009), and Manos (2016)

with lamellate rings or scaly; **scales** imbricate and flattened or tuberculate, not or weakly to markedly reflexed; **chromosome number** **X** = 12. Around 400 species mostly in the Northern Hemisphere (Fig. 2.3).

2.4.2 Subgenus *Quercus*

Receptor-independent sporopollenin masking rugulae in mature pollen grains (Rowley and Claugher 1991; Rowley 1996).

2.4.2.1 Section *Protobalanus* (Intermediate Oaks)

Quercus section *Protobalanus* (Trelease) Schwarz, Notizbl. Bot. Gart. Berlin-Dahlem, 13/116: 21 (1936)

Quercus subgenus *Protobalanus* Trellease, in Standley, Contr. US Natl. Herb. 23:176 (1922).—*Quercus* section *Protobalanus* (Trellease) Camus, Les Chênes, 1: 157 (1938).—*Quercus* section *Protobalanus* (Trellease) Schwarz, Notizbl. Bot. Gart. Berlin-Dahlem, 13/116: 21 (1936) p.p.

Type: *Quercus chrysolepis* Liebm. (Trellease, Proc. Natl. Acad. Sci. 2: 627, 1916; confirmed by Nixon, Ann. Sci. For. 50, suppl. 1: 32s, 1993)

Stamens 8–10, with apiculate apices (Trellease 1924); *pollen ornamentation* weakly verrucate, perforate (Denk and Grimm 2009); footlayer thick and continuous (Denk and Tekleva 2014); styles short to long, elliptic in cross-section; stigmata abruptly dilated; stigmatic surface extending adaxially along stylar suture (Trellease 1924; Manos 1997); fruit maturation biennial (Trellease 1924; Camus 1952–1954; Manos 1997); endocarp tomentose (Trellease 1924; Camus 1952–1954; Manos 1997); position of abortive ovules basal, lateral or apical, can be variable within a single plant (Manos 1997); cup scales triangular and fused at the base, thickened and compressed into rings, often tuberculate and obscured by glandular trichomes, with sharp angled tips; leaf dentitions spinose; wood diffuse porous, tyloses rarely present in vessels of early-wood (Trellease 1924).

Five species in southwestern North America and northwestern Mexico (Manos 1997).

2.4.2.2 Section *Ponticae*

Quercus section *Ponticae* Stefanoff., Ann. Univ. Sofia, ser. 5, 8: 53 (1930)

Quercus ser. *Sadlerianae* Trellease, Oaks of America: 111 (1924).—*Quercus* subsect. *Ponticae* Menitsky (Stefanoff) A.Camus, Bull. Soc. Bot. Fr., 81: 815 (1934).—*Quercus* ser. *Ponticae* Schwarz, Notizbl. Bot. Gart. Berlin-Dahlem, 13/116: 11 (1936).

Lectotype (here designated): *Quercus pontica* K.Koch