

# Chapter 8

## The Anatomy and Functioning of the Xylem in Oaks

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**Abstract** Because of its economic and ecological importance, the genus *Quercus* has been relatively intensively studied for its anatomical and hydraulic characteristics, having often been testing ground for development of methods and hypotheses related to tree structure and function. However, despite long-withstanding interest, we are still far from having obtained a clear understanding of the hydraulic functioning of the species within this genus, the occurrence of trade-offs among various xylem properties and the prevalence of syndromes of characters under different environmental conditions. We conducted a review of the xylem anatomical literature of the genus *Quercus*, an undertaking that does not appear to have been carried out before. We also updated existing quantitative databases of vessel diameter and density, volumetric fractions of parenchyma, wood density and xylem hydraulic properties, to synthesise the main patterns of variation in the hydraulic architecture and functioning of the genus. We found that ring-porous (deciduous) species have lower wood density, higher hydraulic conductivity, xylem that is more vulnerable to embolism and lower Huber values compared to diffuse-porous (evergreen) species. We also report systematic differences among taxonomic groups, with species of sections *Quercus* and *Lobatae* having smaller but more numerous vessels, lower wood density, more vulnerable xylem, higher conductivity and lower Huber values as opposed to species of section *Cerris*. Many of these trends appeared to map onto environmental differences across the three main biomes where *Quercus* species are found, i.e. the temperate, the Mediterranean/semi-arid and the tropical biomes. Although limited by the coverage of the empirical data, our compilation contributes to characterise the hydraulic architecture and functioning of the genus as a function of taxonomic grouping, biome, ring-porosity and leaf phenology. Future investi-

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gations can benefit by the identification of the main factors responsible for these patterns and their likely ecological significance.

## 8.1 Introduction

The xylem is the internal water transport system of plants that links water-absorbing roots to the pores inside the leaves where evaporation takes place. The discipline studying the biophysical and physiological processes controlling how water moves inside the xylem is named hydraulics. Despite having a primary focus on water movement in the xylem, hydraulics also often examines jointly aspects related to the functioning of other hydraulic systems in the stem or in other organs, i.e. root water uptake, radial water transport across the stele, radial water transfer in leaves outside the last xylem conduits up to the sites of evaporation and transport of carbohydrates in the phloem (Tyree and Ewers 1991). Because of its fundamental focus on structural features, hydraulics shares a lot of ground with studies of anatomy and it is often at the interface between these two disciplines that scientific progress has been made.

Studies of the wood anatomy and the hydraulics of the genus *Quercus* have been instrumental in advancing our understanding of the physiological ecology of plant water transport, vulnerability to embolism and plant hydraulic architecture across the plant kingdom. Some of the very early experimental measurements of the physiological bases of plant hydraulic performance were carried out on species of the genus *Quercus*, thereby allowing inferences to be made regarding the realized ecological niches of various species in the field. The first vulnerability curves to drought stress published for a species of the genus *Quercus* was for current-year twigs and petioles of *Quercus rubra* (Cochard and Tyree 1990). The authors employed both hydraulic and acoustic techniques and did not find systematic differences in vulnerability between the two studied organs. Older stems were not examined because “stems had to be cut longer than the longest vessel, and in older stems this meant that we would have to dehydrate stems several meters in length”, an issue we are still grappling with today (see Sect. 8.3.1). More vulnerability curves in response to drought stress followed suit for European oaks (*Quercus petraea*, *Quercus robur* and *Quercus pubescens*—Cochard et al. 1992).

In another relevant early paper, Sperry and Sullivan (1992) reported curves of vulnerability to embolism after freeze-thaw cycles in *Quercus gambelii*. In it, the authors adopted a comparative approach (contrasting diffuse-porous, ring-porous and coniferous species) and highlighted how small tensions above  $-0.2$  MPa were sufficient to embolize 90% of the xylem in the ring-porous *Q. gambelii* following a single freeze-thaw cycle, whereas embolism in diffuse-porous *Betula* and *Populus* species was much lower and almost non-existent in several conifers under the same conditions. Lo Gullo and Salleo (1993) were the first researchers to employ acoustic emissions in Mediterranean *Quercus ilex* to detect loss of hydraulic conductance, documenting subsequent recovery following an irrigation event overnight. They

also investigated the relative sensitivities of this species to freezing and summer drought stresses using hydraulic techniques. Lo Gullo et al. (1995) combined hydraulic techniques with anatomical and staining approaches to determine the relative sensitivities of conduit size in twigs of *Quercus cerris* (larger conduits tended to be more vulnerable), an issue examined also earlier on by Cochard and Tyree (1990) in *Q. rubra*. The concepts of ‘hydraulic constriction zones’ and ‘hydraulic segmentation’ proposed by Zimmermann only a few years before (1983) were also tested experimentally in the early ’90s. Already in 1996, issues related to potential methodological artefacts began to be discussed. In a comparative early analysis of the hydraulics of the genus, Tyree and Cochard (1996) reported that they could not replicate the vulnerability curve for *Q. ilex* published by Lo Gullo and Salleo (1993). Their (Tyree and Cochard 1996) figure 1 gives  $\Psi_{50}$  values (the water potential at which 50% of the maximum hydraulic conductivity is lost) of  $-2.9$  and  $-5.7$  MPa showing a difference between the two studies of almost 3 MPa. Similar differences have been reported later on by other authors (see Sect. 8.3.1).

It is now generally accepted that studies of xylem anatomy and of hydraulic architecture are integral components of the characterization of a species’ ecological niche. A comparative review of the hydraulics of the genus *Quercus* has not been attempted since the early work already cited by Tyree and Cochard (1996), which was limited to six species, while xylem anatomy of oaks has not been reviewed recently. Regarding hydraulics, Tyree and Cochard (1996) concluded their review by stressing the existence of a correlation across species between vulnerability to drought-induced embolism and other indices of drought stress tolerance, while at the same time stating that significant levels of summer embolism are probably avoided in most situations, thanks to an efficient coordination between hydraulic transport system and stomatal control of water loss in leaves. It is therefore obvious already from this initial review (Tyree and Cochard 1996) that a full interpretation of the significance of anatomical and hydraulic relationships in trees needs to incorporate an understanding also of leaf physiology, particularly photosynthesis and stomatal conductance. We therefore recommend reading this chapter in conjunction with the relevant other chapters in this book.

Our objectives for this review were four-fold. Firstly, we reviewed the main elements of vessel anatomy that impinged on xylem function and that allowed a comparative analysis of the genus *Quercus* relative to other angiosperms. We focussed on vessel diameter and its relationship with vessel density, the length of oak water-transporting vessels, the degree of vessel isolation in the wooden matrix (or its reverse, i.e. vessel grouping) and the structure and micro-anatomy of pits (because of their central role in controlling the spread of air emboli) after which we briefly discussed the occurrence of tyloses and their structural and physiological significance. Secondly, we examined tissue-level properties outside of vessel anatomy, i.e. the occurrence and significance of radial and axial parenchyma, and of tracheids and fibres. We ended this section with an overview of the main patterns of variation across the genus in wood density, a central variable that often relates to other physiological and ecological properties. Thirdly, because of the occurrence of very long vessels in oaks, we dedicated a whole section to a critical examination of

the major methodological issues related to the measurement of hydraulic efficiency and hydraulic safety in the genus *Quercus*. Here, we touched on various potential artefacts occurring during hydraulic measurements and we discussed the evidence that these artefacts may have occurred in *Quercus* studies. Fourthly and lastly, we examined the major patterns that have been found across the genus in hydraulic safety (as quantified by xylem  $\Psi_{50}$ ), hydraulic efficiency (as quantified by the sapwood-specific hydraulic conductivity,  $K_{S,max}$ ), minimum values of leaf water potentials encountered in the field ( $\Psi_{min}$ , which partly is an indicator of the maximum levels of soil drought stress encountered at the peak of the seasonal droughts and partly depends on rooting strategies and stomatal behaviour) and the Huber value ( $H_V$ , the ratio between cross-sectional sapwood and leaf area distal to the section, a measure of relative allocation between xylem and leaves).

Because of heterogeneity in data availability, we adopted an opportunistic approach to the content and structuring of the chapter sections. In some cases, our observations primarily have a qualitative nature, attempting to summarise and interpret the variability encountered in the primary literature and place it in context of the species' broader characteristics. In some instances, however, collation of data from the primary literature has already been carried out and global databases are available. In these more fortunate cases (e.g. vessel diameter and density, parenchyma content, wood density, xylem  $\Psi_{50}$ ,  $K_{S,max}$ ,  $\Psi_{min}$  and  $H_V$ ), we carried out a quantitative analysis across the whole genus, focusing on the existence of broad inter-specific patterns. In all these cases, we recognise that our conclusions have a preliminary nature and are primarily limited by the quality and quantity of the available data in the literature.

We also examined the hypothesis that traits are coordinated with one another, thereby supporting the idea that hydraulic strategies represented by syndromes of coordinated traits can be identified within the genus. We examined trends in these various traits in relation to other biological properties of the species, i.e. taxonomic grouping (sub-genera *Cyclobalanopsis* and *Quercus*, and within this last sub-genus, sections *Quercus*, *Lobatae*, *Cerris*, *Mesobalanus* and *Protobalanus*), ring-porosity (classified into ring-porous and diffuse-porous) and leaf phenology (evergreen versus deciduous leaf habit). Finally, we classified all the species we examined into three broad biome classes (tropical, temperate and Mediterranean/semi-arid), following an early biome classification employed for hydraulic traits (Choat et al. 2012). Classification into taxonomic groups and leaf phenology largely follows the Wikipedia list of *Quercus* species (Wikipedia 2017). We recognise that all these classifications are problematic. For ring-porosity, we followed the literature and for dubious cases (semi-ring-porousness), we attempted a classification based on the prevailing opinions from the literature. Where appropriate, we highlighted potential problems associated with the classification we adopted. The following online databases were consulted to resolve borderline cases: The Plant List (2013), Encyclopedia of Life, Wikipedia, Oaks of the World (Hélandot 1987 onwards), eFloras (2008), Tropicos and The Wood Database. Species that The Plant List (2013) classified as belonging to the genera *Cyclobalanus*, *Cyclobalanopsis* or *Lithocarpus* were excluded from the analyses. In Table 8.1, we list the taxonomic

section, biome, ring-porosity type, leaf phenology type and mean values of the selected traits of all the oak species for which we show data in this chapter.

## 8.2 Functional Wood Anatomy

For this section, we explored the variability of the major functional wood traits within the genus *Quercus* and compared structural trait characteristics with other angiosperm genera. Vessel anatomy (ring-porosity, vessel dimensions, vessel packing, network connectivity and tyloses—Sect. 8.2.1) and tissue properties (parenchyma, tracheids and fibres and wood density—Sect. 8.2.2) are discussed.

### 8.2.1 Vessel Anatomy

#### 8.2.1.1 Ring-Porosity

Whether deciduous or evergreen, *Quercus* wood often shows distinct growth rings allowing for dendrochronological analyses. The longest continuous tree-ring chronology in the world is an oak chronology from Southern Germany dating back till 8480 BC (Friedrich et al. 2004; Haneca et al. 2009; Wilson 2010). Although the clearness of the ring boundaries is generally very high for deciduous oak trees from temperate regions due to very pronounced ring-porousness (i.e. large vessels at the beginning of the growing season in contrast to small vessels at the end of it—Wheeler et al. 1989), it might be far less evident how to correctly distinguish annual ring borders for evergreen oaks from Mediterranean or subtropical climates (see some examples in Fig. 8.1). However, several successful attempts have been made (e.g. Cherubini et al. 2003; Gea-Izquierdo et al. 2009) and it has been proven by Campelo et al. (2010) that time series of vessel lumen size in *Q. ilex* trees from Catalonia (Spain) bear climatic signals that can be used for dendrochronology and climate reconstruction in combination with the more classical tree-ring width data, creating opportunities for oak species falling within the gradient from semi-ring-porousness (i.e. intermediate condition between ring-porousness and diffuse-porousness—Wheeler et al. 1989) to diffuse-porousness (i.e. homogenous vessel size distribution over the growth rings—Wheeler et al. 1989). The relationships deciduousness/ring-porousness and evergreenness/diffuse-porousness are often but not always true within the *Quercus* genus (see some examples in Table 8.1). In the quantitative analyses conducted for this chapter, the relation of ring-porosity to other hydraulic traits is examined since it is a crucial aspect of oak xylem structure and thus hydraulics.

Table 8.1 List of all the *Quercus* species employed in the quantitative analyses presented in this chapter

Species	Section	Biome	Porosity	Phenology	$\Psi_{50}$	$K_{S,max}$	$H_V$	WD	$\Psi_{min}$	$D_{mean}$	$N_{cond}$	$P_{rad}$	$P_{ax}$	$P_{tot}$
<i>Quercus acuta</i>	Cyclobalanopsis	TMS	Diffuse-porous	E								23.30		
<i>Quercus acutissima</i>	Cerris	TRS	Ring-porous	D	-3.39	2.42		0.74		72.48	7.43	21.90		
<i>Quercus agrifolia</i>	Lobatae	WDS	Diffuse-porous	E	-1.89	4.05		0.62	-3.12	50.88				
<i>Quercus alba</i>	Quercus	TMS	Ring-porous	D	-1.37	1.37	1.45E-04	0.62	-1.14	52.06	43.40	22.83	12.48	35.32
<i>Quercus aliena</i>	Quercus	TMS	Ring-porous	D	-2.09	6.30		0.69						
<i>Quercus aquifolioides</i>	Quercus	TRS		E				0.79						
<i>Quercus argentata</i>	Cyclobalanopsis	TRS		E				0.74						
<i>Quercus arizonica</i>	Quercus	WDS	Ring-porous	E				0.59						
<i>Quercus asymetrica</i>	Cyclobalanopsis	TRS		E				0.88						
<i>Quercus austrina</i>	Quercus	TMS	Ring-porous	D		1.90	1.83E-04	0.75	-2.99					
<i>Quercus berberidifolia</i>	Quercus	WDS		E	-2.16	1.83	8.04E-04	0.70	-4.35	44.56	36.65			
<i>Quercus bicolor</i>	Quercus	TMS	Ring-porous	D				0.65				29.72		
<i>Quercus blakei</i>	Cyclobalanopsis	TRS		E				0.78						
<i>Quercus calliprinos</i>	Cerris	WDS	Diffuse-porous	E						78.00	15.00			
<i>Quercus canariensis</i>	Quercus	WDS	Ring-porous	D						43.63	49.85			
<i>Quercus candicans</i>	Lobatae	TRS	Ring-porous	D								21.90		
<i>Quercus castaneifolia</i>	Cerris	TMS	Ring-porous	D						121.50	7.14			
<i>Quercus cerris</i>	Cerris	WDS	Ring-porous	D				0.70		122.45	7.19			
<i>Quercus chapmanii</i>	Quercus	TMS		D	2.50		1.35E-04	0.78	-2.10					
<i>Quercus chevalieri</i>	Cyclobalanopsis	TRS		E				0.69						
<i>Quercus chrysolepis</i>	Protobalanus	WDS	Diffuse-porous	E				0.70						
<i>Quercus chungii</i>	Cyclobalanopsis	TRS		E				0.78						
<i>Quercus coccifera</i>	Cerris	WDS	Diffuse-porous	E	-6.96	0.29	7.59E-04		-10.30	48.70	56.60			

(continued)

Table 8.1 (continued)

Species	Section	Biome	Porosity	Phenology	$\Psi_{50}$	$K_{S,max}$	$H_V$	WD	$\Psi_{min}$	$D_{mean}$	$N_{cond}$	$P_{rad}$	$P_{ax}$	$P_{tot}$
<i>Quercus coccolinea</i>	Lobatae	TMS	Diffuse-porous	E				0.61				18.15	23.30	41.45
<i>Quercus cornelius-mulleri</i>	Quercus	WDS		E	-0.70	2.03	5.06E-04	0.68	-4.50					
<i>Quercus costaricensis</i>	Lobatae	TRS		E				0.61						
<i>Quercus crenata</i>	Cerris	WDS		E								9.05		
<i>Quercus delavayi</i>	Cyclobalanopsis	TRS		E				0.78						
<i>Quercus douglasii</i>	Quercus	WDS	Diffuse-porous	D				0.59		65.41	11.41			
<i>Quercus ellipsoidalis</i>	Lobatae	TMS		D				0.59						
<i>Quercus emoryi</i>	Lobatae	WDS	Ring-porous	D	-1.40	1.61	4.97E-05	0.59	-2.36					
<i>Quercus engelmannii</i>	Quercus	WDS		E				0.59						
<i>Quercus engelriana</i>	Quercus	WDS		E				0.72						
<i>Quercus fabri</i>	Quercus	TRS	Ring-porous	D	-5.14	3.15		0.67		38.03				
<i>Quercus faginea</i>	Quercus	WDS	Ring-porous	D			2.16E-04			61.04	94.07			
<i>Quercus falcata</i>	Lobatae	TMS	Ring-porous	D	-0.92	2.75	1.87E-04	0.59	-2.46	45.82		18.75	27.60	46.30
<i>Quercus fleuryi</i>	Cyclobalanopsis	TRS		E				0.81						
<i>Quercus frainetto</i>	Mesobalanus	WDS	Ring-porous	D	-4.56				-3.13	31.86	107.00			
<i>Quercus fusiformis</i>	Quercus	WDS	Diffuse-porous	E	-0.50	1.70				45.40				
<i>Quercus gambelii</i>	Quercus	WDS	Ring-porous	D	-0.58	2.00	3.90E-05	0.62	-2.16	30.93				
<i>Quercus garryana</i>	Quercus	TMS	Diffuse-porous	D	-3.61			0.64		48.47	36.90	13.50	11.00	24.50
<i>Quercus gemelliflora</i>	Cyclobalanopsis	TRS		E				0.70						
<i>Quercus geminata</i>	Quercus	TMS	Ring-porous	E		1.70	4.95E-04	0.87	-3.23					
<i>Quercus gilva</i>	Cyclobalanopsis	TRS		E				0.80						
<i>Quercus glauca</i>	Cyclobalanopsis	TRS	Diffuse-porous	E				0.73		128.00	4.00			

(continued)

Table 8.1 (continued)

Species	Section	Biome	Porosity	Phenology	$\Psi_{50}$	$K_{S,max}$	$H_V$	WD	$\Psi_{min}$	$D_{mean}$	$N_{cond}$	$P_{rad}$	$P_{ax}$	$P_{tot}$
<i>Quercus glaucooides</i>	Quercus	WDS	Diffuse-porous	E				0.80						
<i>Quercus graciliformis</i>	Lobatae	WDS		D				0.59						
<i>Quercus griffithii</i>	Quercus	TRS		D				0.68						
<i>Quercus grisea</i>	Quercus	WDS	Ring-porous	D	-1.69	1.73	4.98E-05	0.59	-3.41					
<i>Quercus hemisphaerica</i>	Lobatae	TMS	Ring-porous	E		2.80	2.25E-04	0.69	-2.13					
<i>Quercus hypoleucoides</i>	Lobatae	WDS	Ring-porous	E	-0.93	2.16	3.83E-05	0.59	-2.39					
<i>Quercus ilex</i>	Quercus	WDS	Diffuse-porous	E	-4.66	0.89	3.64E-04	0.75	-3.75	39.47	72.83	34.10		
<i>Quercus ilicifolia</i>	Lobatae	TMS		D				0.59						
<i>Quercus imbricaria</i>	Lobatae	TMS		D				0.59						
<i>Quercus incana</i>	Lobatae	TMS	Ring-porous	D		3.20	2.04E-04	0.67	-2.86					
<i>Quercus infectoria</i>	Cerris	WDS	Diffuse-porous	E						115.00	40.00			
<i>Quercus ilhaburensis</i>	Cerris	WDS	Diffuse-porous	D						125.00	8.00			
<i>Quercus kelloggii</i>	Lobatae	TMS	Ring-porous	D				0.51						
<i>Quercus laevis</i>	Lobatae	TMS	Ring-porous	D	-1.89	1.60	2.09E-04	0.64	-2.72	51.34				
<i>Quercus lamellosa</i>	Cyclobalanopsis	TRS	Ring-porous	E						138.00	4.00			
<i>Quercus lanata</i>	Quercus	TRS		E						113.00	7.00			
<i>Quercus langbianensis</i>	Cyclobalanopsis	TRS		E				0.81						
<i>Quercus laurifolia</i>	Lobatae	TMS	Ring-porous	E		5.20	1.38E-04	0.58	-2.70			18.85	26.35	45.20
<i>Quercus laurina</i>	Lobatae	WDS	Ring-porous	E				0.70						
<i>Quercus leucotrichophora</i>	Quercus	TRS		E						128.00	7.00			
<i>Quercus lobata</i>	Quercus	WDS	Ring-porous	D				0.55		70.23	31.97			

(continued)

Table 8.1 (continued)

Species	Section	Biome	Porosity	Phenology	$\Psi_{50}$	$K_{S,max}$	$H_V$	WD	$\Psi_{min}$	$D_{mean}$	$N_{cond}$	$P_{rad}$	$P_{ax}$	$P_{tot}$
<i>Quercus lusitanica</i>	Quercus	WDS	Ring-porous	D				0.70						
<i>Quercus lyrata</i>	Quercus	TMS	Ring-porous	D				0.57						
<i>Quercus macrocarpa</i>	Quercus	TMS	Ring-porous	D				0.58		39.54	37.28	20.60	12.00	32.60
<i>Quercus margarettae</i>	Quercus	TMS		D		1.70	2.40E-04	0.70	-3.34					
<i>Quercus marilandica</i>	Lobatae	TMS	Ring-porous	D				0.69				21.55	23.75	45.30
<i>Quercus michauxii</i>	Quercus	TMS	Ring-porous	D	-1.70	4.40	1.11E-04	0.64	-2.91	41.83		25.30		
<i>Quercus minima</i>	Quercus	TMS		E		4.20	3.09E-04	0.79						
<i>Quercus mongolica</i>	Quercus	TMS	Ring-porous	D		0.50	2.28E-04	0.60	-0.96	129.84	18.24	12.80		
<i>Quercus montana</i>	Quercus	TMS	Ring-porous	D				0.57						
<i>Quercus morii</i>	Cyclobalanopsis	TMS	Diffuse-porous	E				0.80						
<i>Quercus muhlenbergii</i>	Quercus	TMS		D				0.59						
<i>Quercus multinervis</i>	Cyclobalanopsis	TMS		E				0.76						
<i>Quercus myrsinifolia</i>	Cyclobalanopsis	TRS		E				0.77						
<i>Quercus myrtifolia</i>	Lobatae	TMS		E	-0.75	1.70	2.64E-04	0.81	-2.46			21.75		
<i>Quercus nigra</i>	Lobatae	TMS	Ring-porous	E	-1.31	2.70	1.82E-04	0.63	-1.95	43.91		23.45	25.95	44.55
<i>Quercus oblongata</i>	Cyclobalanopsis	TRS	Diffuse-porous	E				0.68						
<i>Quercus oblongifolia</i>	Quercus	TMS		E				0.59						
<i>Quercus oglethorpensis</i>	Quercus	TMS	Ring-porous	D				0.59						
<i>Quercus oleoides</i>	Quercus	TRS	Ring-porous	E	-3.03	2.10	1.18E-04	0.86	-3.47					

(continued)

Table 8.1 (continued)

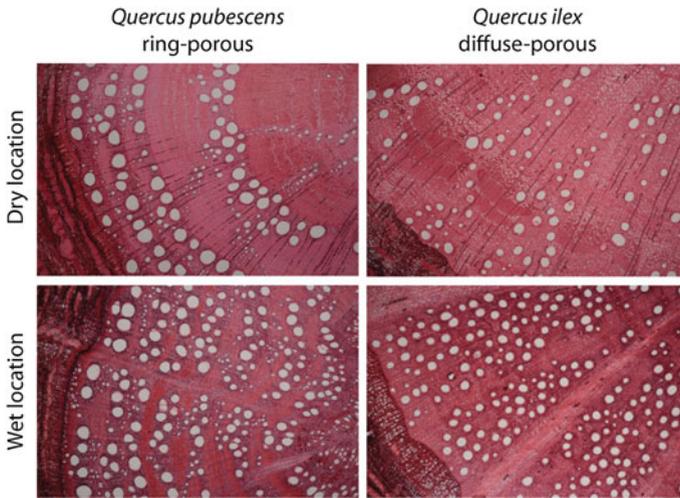
Species	Section	Biome	Porosity	Phenology	$\Psi_{50}$	$K_{S,max}$	$H_V$	WD	$\Psi_{min}$	$D_{mean}$	$N_{cond}$	$P_{rad}$	$P_{ex}$	$P_{tot}$
<i>Quercus oxyodon</i>	Cyclobalanopsis	TRS		E						118.00	7.00			
<i>Quercus pachyloma</i>	Cyclobalanopsis	TMS		E				0.73						
<i>Quercus pagoda</i>	Lobatae	TMS		D				0.61				17.80	24.05	41.85
<i>Quercus palustris</i>	Lobatae	TMS	Ring-porous	D				0.58						
<i>Quercus petraea</i>	Quercus	TMS	Ring-porous	D	-3.06			0.57	-3.17					
<i>Quercus phellos</i>	Lobatae	TMS	ring-porous	D	-1.42	1.35	1.81E-04	0.60	-1.97	49.17				
<i>Quercus phillyraeoides</i>	Cerris	TRS	Diffuse-porous	E				0.69		41.48	14.65			
<i>Quercus prinoides</i>	Quercus	TMS		D				0.59						
<i>Quercus pubescens</i>	Quercus	WDS	Ring-porous	D	-2.88	1.58			-4.20					
<i>Quercus pumila</i>	Lobatae	TMS		E		3.00	1.68E-04	0.71						
<i>Quercus pyrenaica</i>	Mesobalanus	TMS	Ring-porous	D				0.84						
<i>Quercus robur</i>	Quercus	TMS	Ring-porous	D	-1.90	1.30		0.57	-2.94	43.12	39.37	17.54	17.20	33.95
<i>Quercus rubra</i>	Lobatae	TMS	Ring-porous	D	-2.23	1.33	1.75E-04	0.60	-1.30	45.11	11.62	16.88	14.05	31.01
<i>Quercus rugosa</i>	Quercus	TRS		E				0.60						
<i>Quercus salicifolia</i>	Lobatae	TRS		E				0.67						
<i>Quercus sebifera</i>	Quercus	WDS		E	-5.50	0.71	2.45E-04	0.71	-5.58					
<i>Quercus semecarpifolia</i>	Cerris	TRS		E						173.00	5.00			
<i>Quercus semiserrata</i>	Cyclobalanopsis	TRS	Diffuse-porous	E				0.71						
<i>Quercus serrata</i>	Quercus	TRS	Ring-porous	D	-2.70	2.87		0.68		27.34				
<i>Quercus sessilifolia</i>	Cyclobalanopsis	TMS		E				0.68						
<i>Quercus shumardii</i>	Lobatae	TMS	Ring-porous	D		3.70	1.32E-04	0.63	-2.40			17.90	23.60	41.50
<i>Quercus sideroxylla</i>	Quercus	TRS						0.63						
<i>Quercus similis</i>	Quercus	TMS		D				0.59						
<i>Quercus sinuata</i>	Quercus	WDS	Ring-porous	D				0.59		37.00				

(continued)

Table 8.1 (continued)

Species	Section	Biome	Porosity	Phenology	$\Psi_{50}$	$K_{S,max}$	$H_V$	WD	$\Psi_{min}$	$D_{mean}$	$N_{cond}$	$P_{rad}$	$P_{ax}$	$P_{tot}$
<i>Quercus stellata</i>	Quercus	TMS	Ring-porous	D	-0.82	1.86	1.77E-04	0.68		47.24		19.15	29.75	48.90
<i>Quercus suber</i>	Cerris	WDS	Diffuse-porous	E	-3.68	1.03		0.77	-2.97	54.52	99.27			
<i>Quercus subsericea</i>	Cyclobalanopsis	TRS		E				0.77						
<i>Quercus texana</i>	Lobatae	TMS		D				0.59						
<i>Quercus turbinella</i>	Quercus	TMS	Ring-porous	D	-0.50									
<i>Quercus variabilis</i>	Cerris	TMS	Ring-porous	D				0.76		110.58	5.36			
<i>Quercus velutina</i>	Lobatae	TMS	Ring-porous	D				0.56				25.15	21.80	46.95
<i>Quercus virginiana</i>	Quercus	TMS	Diffuse-porous	E		3.00	3.63E-04	0.86	-2.17			32.20		
<i>Quercus wislizeni</i>	Lobatae	WDS	Diffuse-porous	E	-1.69	1.56		0.66	-3.57	39.61	37.30			

Selected anatomical, tissue-level and hydraulic traits were summarised from available databases enlarged with additional more recent literature. See text for further details  
 Notes Nomenclature follows The Plant List (2013). Codes for biomes: TMS temperate; TRS tropical; WDS Mediterranean/semi-arid. For leaf phenology: D deciduous, E evergreen.  
 $\Psi_{50}$ , water potential at 50% loss of hydraulic conductivity (MPa);  $K_{S,max}$  maximum sapwood-specific hydraulic conductivity ( $kg\ m^{-1}\ MPa^{-1}\ s^{-1}$ );  $H_V$ , Huber value; WD, wood density ( $g\ cm^{-3}$ );  $\Psi_{min}$ , minimum water potential experienced in the field (MPa);  $D_{mean}$ , mean vessel diameter ( $\mu m$ );  $N_{cond}$ , mean vessel density ( $mm^{-2}$ );  $P_{rad}$ , % radial parenchyma;  $P_{ax}$ , % axial parenchyma;  $P_{tot}$ , % axial plus radial parenchyma



**Fig. 8.1** Exemplary transverse sections of ring-porous *Quercus pubescens* (left) and diffuse-porous *Quercus ilex* (right) branch wood taken from trees growing at a dry (top) and a wet (bottom) location in Catalonia, Spain. Classification of the study sites into dry or wet was based on species-specific terciles in the range of average annual precipitation over potential evapotranspiration ratios. Sections are about 20 micrometres thick and were stained with a safranin–astra blue mixture. Images are 1.1 by 0.7 mm (top, left) and 2.2 by 1.4 mm (top, right and bottom)

### 8.2.1.2 Vessel Size and Density

Conduit size and density are perhaps the two most widely measured anatomical characteristics of trees. These two traits have a direct impact on xylem hydraulic efficiency, particularly through the fourth-power relationship between lumen hydraulic conductivity and conduit diameter (Tyree and Zimmermann 2002). Vessel size and density define the lumen fraction of a wood section (via their multiplication) and the variation in vessel composition within the potential transport space (their ratio). A global dataset compiled by Zanne et al. (2010) revealed that hydraulic conductivity is more sensitive to changes in the total lumen fraction than to changes in the size to number ratio, all other factors being equal. However, the vessel composition ratio was the driving factor for potential conductivity differences across species.

To assess vessel characteristics of oaks in comparison with other angiosperm species, we extended the dataset of Zanne et al. (2010) with data from Jacobs (2013) and with anatomy data present in an updated version of the global xylem traits database (Choat et al. 2012) (Table 8.1). Values were averaged at the species level prior to analysis. Only measurements conducted on stems were considered, as measurements on other organs were extremely rare. It should be noted, however, that the few studies measuring vessel dimensions in stems and roots of the same oak individuals have reported much wider conduits in the latter organ, particularly in

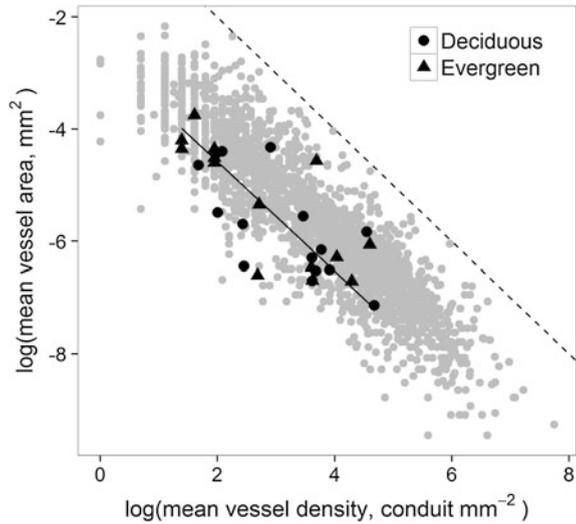
deep roots, consistent with results for other plant groups (Martínez-Vilalta et al. 2002; McElrone et al. 2004). The mean vessel diameter in deep (7–20 m) roots of *Quercus fusiformis* and *Quercus sinuata* was around 100  $\mu\text{m}$ , with maximum values over 200  $\mu\text{m}$  that allowed seeing the conduits with the naked eye (McElrone et al. 2004).

According to our dataset, average vessel diameter ( $D_{mean}$ ) in oak stems is  $62 \pm 5 \mu\text{m}$  ( $N = 42$  species) (mean  $\pm$  SE; calculated in all cases after back-transformation from log-transformed data) and the average vessel density ( $N_{cond}$ ) is  $19 \pm 4$  conduits $\cdot\text{mm}^{-2}$  ( $N = 30$  species). The former value is close to the average for non-oak angiosperm species ( $68 \pm 1 \mu\text{m}$ ,  $N = 2204$  non-oak species in Zanne et al. 2010), whereas vessel density is clearly lower for oaks relative to other angiosperms ( $38 \pm 1$  conduits $\cdot\text{mm}^{-2}$ ,  $N = 2204$  non-oak species). However, these comparisons must be interpreted with care, particularly for vessel diameters, as there are substantial methodological differences in how this variable can be measured, which were not accounted for in our compilation from disparate literature sources. If only the data from the Zanne et al. (2010) database are considered, including 13 oak species, the low average vessel density for oaks was supported ( $19 \pm 4$  conduits $\cdot\text{mm}^{-2}$  for oaks), whereas vessel diameter appeared to be larger for oaks ( $99 \pm 18 \mu\text{m}$ ) than for other angiosperms.

We assessed the effect of taxonomic grouping, species biome, ring-porosity and leaf phenology on  $\log(D_{mean})$  and  $\log(N_{cond})$  using linear models with one explanatory variable at a time (as the strong association among them prevented including them in a single, multiple regression model). For vessel diameter, only taxonomic section had a significant effect ( $P < 0.001$ ), with species from the *Cyclobalanopsis* ( $N = 3$ ) and *Cerris* ( $N = 11$ ) groups having larger vessels than those in sections *Quercus* ( $N = 20$ ) and *Lobatae* ( $N = 7$ ). The only species in section *Mesobalanus* (*Quercus frainetto*) had the smallest vessels. The effect of taxonomic section was also significant for vessel density ( $P = 0.015$ ), with sections *Mesobalanus* ( $N = 1$ ) and *Quercus* ( $N = 13$ ) having higher values than *Cyclobalanopsis* ( $N = 3$ ), whereas *Cerris* ( $N = 11$ ) and *Lobatae* ( $N = 2$ ) had intermediate values. The only other variable with a significant effect on oak vessel density was biome ( $P < 0.001$ ). Temperate ( $N = 8$ ) and Mediterranean/Semi-arid species ( $N = 14$ ) had higher conduit density than tropical species ( $N = 8$ ). Larger vessels in the *Cyclobalanopsis* and *Cerris* groups are probably associated with higher vulnerability to freezing-induced embolism (Davis et al. 1999), although these differences are not reflected in clear bioclimatic segregation among phylogenetic sections (Cavender-Bares et al. 2004).

We assessed the relationship between vessel size and density after converting vessel diameter into area, for consistency with previous work and because the product of vessel area and density is a direct measure of the lumen fraction (Zanne et al. 2010). Oak species occupy a substantial range of the angiosperm space in the relationship between vessel area and density, although they tend to cluster towards the lower vessel density end (Fig. 8.2). Interestingly, oaks tend to have small vessels for a given vessel density, relative to other angiosperms, implying a lower lumen fraction. The fact that oak species tend to be located far from the packing

**Fig. 8.2** Relationship between mean vessel area and mean vessel density for oak species represented on top of the scatterplot for all angiosperms (the latter obtained from Zanne et al. 2010). Both variables are (natural) log-transformed. Symbol shapes distinguish between deciduous and evergreen oak species. The solid line indicates the standardized major axis regression between the two variables (slope =  $-0.97$ ). The dashed line indicates the packing limit, corresponding to a lumen fraction of 1



limit indicates the importance of the ground tissue, whether genetically defined or as an adaptation for survival (Jupa et al. 2016), and the tendency of the genus towards xylem structures that provide high mechanical support. The relationship between vessel area and density for oaks was not affected by taxonomic grouping, species biome, ring-porosity or leaf phenology.

### 8.2.1.3 Vessel Length

Vessel length is a key trait in woody plant hydraulics due to its defining role in affecting both hydraulic safety and efficiency (Lens et al. 2011; Jacobsen et al. 2012). Jacobsen et al. (2012) found average vessel length in the Fagaceae to be smaller than 0.2 m, as was the case for most of the 31 studied species. However, oaks are often mentioned as being long-vesselled (e.g. *Q. gambelii* and *Quercus prinus*—Hacke et al. 2006; *Q. robur*—Cochard et al. 2010; *Q. ilex*—Martínez-Vilalta et al. 2002 and Martin-StPaul et al. 2014; *Quercus variabilis*—Pan et al. 2015). Comparative studies show indeed that *Q. gambelii* has much longer vessels than *Betula occidentalis* and *Populus tremuloides* (Sperry and Sullivan 1992) and that *Q. robur* had the longest vessels in a group of ten woody angiosperms (Cochard et al. 2010). Sperry and Sullivan (1992) show a length distribution of *Q. gambelii* vessels in which almost 40% falls in the 5–10 cm length class and 5% in the 65–70 cm maximum class. But *Quercus* vessels are not always the

longest. The maximum vessel length of *Q. ilex* ( $0.45 \pm 0.01$  m) is only second in a list of nine studied species, after *Eucalyptus camaldulensis* ( $0.52 \pm 0.06$  m) (Trifilò et al. 2015). *Q. rober* had similar maximum vessel length compared to *Vitis vinifera* and *Populus trichocarpa* in a study where its mean vessel length was also the same as for *V. vinifera* but six times larger than in *P. trichocarpa* (Venturas et al. 2016). In Table 8.2, we extended the mean and maximum vessel length data coverage provided in Appendix S1 of Jacobsen et al. (2012). It must be noticed that different measurement methods can generate different outcomes even in the same individuals (Pan et al. 2015; Oberle et al. 2016) and that within-tree and within-species variability might be larger than considered so far (Wang et al. 2014; Zhang and Holbrook 2014; Pan et al. 2015).

#### 8.2.1.4 Vessel Grouping

Oak wood is known for having a high degree of solitary vessels, arranged in a diagonal/oblique (intermediate between radially and tangentially) or a dendritic pattern (Wheeler et al. 1989; Johnson et al. 2014; InsideWood 2004 onwards; Ellmore et al. 2006; Sano et al. 2008; Mencuccini et al. 2010; Kim and Daniel 2016a; Venturas et al. 2016). Mencuccini et al. (2010) classified *Q. petraea* and *Q. robur* as species with an overall random vessel distribution (as opposed to aggregated or uniform) with the note that there is a difference between the early-wood (random) and the late-wood (clustered) vessel distribution in these ring-porous species. Three-dimensional analysis of roots of *Q. fusiformis* showed that only 1 (shallow roots) to 6 (deep roots) % of the vessels were connected to other vessels, a finding that is likely related to the high resistance to embolism of this species' roots relative to other species with more vessel connections (Johnson et al. 2014). In addition, dye experiments in saplings of *Q. rubra* showed high sectoriality and low potential radial flow, attributed to the low degree in radial and tangential vessel interconnections (Ellmore et al. 2006). Lateral connections between vessels and their surrounding non-vascular cells such as ray parenchyma and vasicentric tracheids might thus ensure network connectivity, as has been observed for *Quercus suber* (Sousa et al. 2009) and other Mediterranean oak species (*Q. ilex*, *Quercus pyrenaica* and *Quercus faginea*—cf. Sousa et al. 2009).

#### 8.2.1.5 Pits

The structural variability of intervessel pits—the tiny cavities in the secondary cell walls that allow water and air passage between adjacent vessels (Sperry and Tyree 1988; Choat et al. 2008; Jansen et al. 2009; Schenk et al. 2015)—has not been

**Table 8.2** Mean and maximum vessel length data of *Quercus* species as found in literature

Species	Sample information	Mean vessel length (m)	Maximum vessel length (m)	References
<i>Quercus agrifolia</i>	Stems from adult shrubs		1.96	Jacobsen et al. (2007)
<i>Quercus alba</i>	Branches from adult trees	0.1153		Cochard and Tyree (1990)
	Model estimate	0.025		Oberle et al. (2016)
<i>Quercus berberidifolia</i>	Stems from adult Shrubs	0.1779	1.60	Jacobsen et al. (2007), Hacke et al. (2009)
<i>Quercus gambelii</i>	Branches from adult trees	0.1656	0.65 – 0.70	Sperry and Sullivan (1992)
	Stems from adult trees			Hacke et al. (2006)
<i>Quercus ilex</i>	Stems from adult trees		0.96 ± 0.07	Martínez-Vilalta et al. (2002)
	Current year sprouts	0.86	0.75 – 1.00	Martin-StPaul et al. (2014)
	Stems of young trees (>15y)		0.45 ± 0.01	Trifilò et al. (2015)
<i>Quercus prinus</i>	Stems from adult trees	0.1571		Hacke et al. (2006)
<i>Quercus robur</i>	Terminal shoots		1.34 ± 0.38	Cochard et al. (2010)
	Branches from young trees	0.109 ± 0.019	0.830 ± 0.186	Venturas et al. (2016)
<i>Quercus rubra</i>	Branches from adult trees	0.1159		Cochard and Tyree (1990)
	Model estimate	0.075		Oberle et al. (2016)
<i>Quercus variabilis</i>	Stem from mature trees (method 1a)	0.1059 ± 0.0077		Pan et al. (2015)
	Stem from mature trees (method 1b)	0.2106 ± 0.0075		Pan et al. (2015)
	Stem from mature trees (method 2)	0.4549 ± 0.0065		Pan et al. (2015)
<i>Quercus velutina</i>	Model estimate	0.06		Oberle et al. (2016)
<i>Quercus wislizenii</i>	Stems of adult shrubs		1.45	Jacobsen et al. (2007)

The table is an extended version from Jacobsen et al. (2012) (Appendix S1)

extensively studied in general, with oaks not being an exception. This is mainly due to the minuscule nature of pits and the difficulty to access them (mostly by electron microscopy). Table 8.3 gives an overview of the published data on oak pit features (intervessel and other pit types) that play a role in determining how easily liquid or air can pass from one cell to another within the transport network (Lens et al. 2011).

Table 8.3 Overview of *Quercus* pit structural characteristics

Species	Sample information	Pit diameter—horizontal (µm)	Pit diameter—longitudinal (µm)	Pit aperture area (µm <sup>2</sup> )	Pit membrane thickness (nm)	Total inter-vessel cell wall thickness (nm)	References
<b>Vessel connections</b>							
<i>Quercus fusiformis</i>	Shallow roots			3.59 ± 0.29	239 ± 30		Johnson et al. (2014)
	Deep roots			18.85 ± 2.71	410 ± 40		
<i>Quercus ilex</i>		5.73		2.01	689		Choat et al. (2012) (updated)
<i>Quercus robur</i>	Last growth ring of young branches	5.886 ± 0.75			278 ± 87	2503 ± 562	Jansen et al. (2009)
<i>Quercus rubra</i>	Branches of mature trees	6–10					Ellmore et al. (2006)
<i>Quercus serrata</i>	Stems of mature trees—early wood			5.67 ± 2.16	163.79		Ahmed et al. (2011)
	Stems of mature trees—late wood			1.95 ± 0.88			
<b>Tracheid connections</b>							
<i>Quercus crispula</i>	Outer sapwood	6.0 ± 0.47	5.9 ± 0.57				Sano and Jansen (2006)
<i>Quercus hypoleucoides</i>		11.3 by 26.5					Adaskaveg et al. (1995)

(continued)

Table 8.3 (continued)

Species	Sample information	Pit diameter—horizontal (µm)	Pit diameter—longitudinal (µm)	Pit aperture area (µm <sup>2</sup> )	Pit membrane thickness (nm)	Total inter-vessel cell wall thickness (nm)	References
<b>Vessel-tracheid connections</b>							
<i>Quercus crispula</i>	Stem of mature trees—early wood	5.7 ± 0.61	5.2 ± 0.80				Sano et al. (2008)
	Stem of mature trees—late wood	5.8 ± 0.77	5.7 ± 0.79				
<b>Fibre connections</b>							
<i>Quercus crispula</i>	Outer sapwood	2.2 ± 0.40	2.5 ± 0.36				Sano and Jansen (2006)
<i>Quercus serrata</i>	Stems of mature trees—early wood			1.35 ± 0.57			Ahmed et al. (2011)
	Stems of mature trees—late wood			1.08 ± 0.51			
<b>Ray connections</b>							
<i>Quercus serrata</i>	Stems of mature trees—early wood			0.90 ± 0.72	312.48		Ahmed et al. (2011)
	Stems of mature trees—late wood			0.68 ± 1.53			

### Intervessel Pits—Arrangement and Size

According to the available information, intervessel pits in oaks mostly seem to be alternately organised, i.e. in diagonal rows (Wheeler et al. 1989; InsideWood 2004 onwards; Jansen et al. 2009). However, Ellmore et al. (2006) reported the oval and widely scattered pits of *Q. rubra* to only be vaguely alternate and intervessel pits in the roots of *Q. fusiformis* were observed to be mostly alternate but occasionally also scalariform or gash-like (Johnson et al. 2014). In a comparative study on 26 hardwood species, average pit diameter of *Q. robur* fell within the top half of all observed values (5.9  $\mu\text{m}$ , species range: 2.1–7.6  $\mu\text{m}$ ) (Jansen et al. 2009) and in comparison to poplar (*Populus tomentiglandulosa*), *Quercus serrata* had wider pit apertures (Ahmed et al. 2011). Vessel walls of *Q. rubra* branches were for 12% occupied by intervessel pits (Ellmore et al. 2006) and roots of *Q. fusiformis* for 6–7% (Johnson et al. 2014). However, Christman et al. (2012) found only 7% of the intervessel pits in *Q. gambelii* to be air-seeding. It has been suggested by these authors that ring-porous species such as *Q. gambelii* compensate their large leakiness probability at the pit level that comes with the highly efficient, large vessels in their early-wood, with a low degree of vessel connectivity, thicker pit membranes or with refilling (Christman et al. 2012).

### Intervessel Pits—Pit Membranes

Pore sizes in intervessel pit membranes have a large effect on both the hydraulic conductivity of the xylem and its vulnerability to embolism (Wheeler et al. 2005). Dye experiments in *Q. rubra* confirmed that pitting alone cannot explain intervascular liquid transfer pointing to the role of pit membrane porosity (Ellmore et al. 2006). Jansen et al. (2009) found pit membranes of *Q. robur* to be without visible pores on Scanning Electron Microscopy (SEM) images, in contrast to most other studied hardwood species, and observed a species characteristic pit membrane thickness (Table 8.3) that fell within the average thickness of 100–300 nm. In the roots of *Quercus fusilis*, pit membranes did not show any visible pores either (Johnson et al. 2014). Theoretically estimated pit membrane pore diameters were  $0.134 \pm 0.02 \mu\text{m}$  for shallow and  $0.167 \pm 0.02 \mu\text{m}$  for deep roots (Johnson et al. 2014). Pit membranes were thicker in deep than in shallow roots, accounting for a larger portion of the overall xylem hydraulic resistance (Johnson et al. 2014).

### Other Pit Types

Sano et al. (2008) studied other pit types and found that pit pairs between vessels and fibres and between vessels and vasicentric tracheids were frequently present in *Quercus crispula* (vessel-tracheid connections: 88.2 pairs per 10,000  $\mu\text{m}^2$  on the radial wall for early-wood and 49.0 for late-wood), with the pit membranes observed as sheet-like, homogeneous and without visible pores. Bordered pits were

observed between vessels and tracheids in *Q. robur* by Kim and Daniel (2016a). The high density of vessel-fibre/tracheid connections in *Q. crispula*, in contrast to other studied species, was attributed to the species' high degree of solitary vessels, with tracheary elements thus supposed to contribute to the transpiration flow (Sano et al. 2008).

There is a consistent structural difference in pits between fibres and pits between tracheids that can be attributed to their functional roles in support and conduction, respectively (Sano and Jansen 2006). Interfibre pits were found to be smaller than 4  $\mu\text{m}$  and very often showed simple or multiple perforations (studies on *Q. crispula* and *Q. robur*, Sano and Jansen 2006; Kim and Daniel 2016a). Intertracheid pits in *Q. crispula* on the other hand were larger than 4  $\mu\text{m}$  and their membranes were densely and evenly packed with microfibrils, only for 10% showing sparsely packed microfibril regions at the membrane periphery (Sano and Jansen 2006). Thickened walls have also been observed in bordered tracheid pits of *Quercus hypoleucoides* (Adaskaveg et al. 1995).

Pits in *Q. robur* were found to be half-bordered between tracheary elements and parenchyma cells and simple between parenchyma cells (Kim and Daniel 2016a). Roots of *Q. fusiformis* showed scalariform vessel-parenchyma pitting, interspersing and surrounding inter-vessel and vessel-tracheid alternate pitting (Johnson et al. 2014). Heavily encrusted parenchyma pit membranes were observed in *Q. serrata* (Ahmed et al. 2011). Early- and late-wood of *Q. robur* were contrasting in the abundance of pits associated with axial and radial parenchyma, with the former being more abundant in the earlywood and the latter being more abundant in the late-wood (Kim and Daniel 2016a).

Pit membrane chemistry showed large variability, both between pit types and between early- and late-wood in *Q. robur* (Kim and Daniel 2016a, b). However, the functional significance of this variability is yet to be elucidated. It was suggested that the presence of hemicelluloses in the inter-tracheid and tracheid-vessel pits could play a similar role as pectin, i.e. mediate pit membrane porosity through changes in ion concentrations (Kim and Daniel 2016a, b).

### 8.2.1.6 Tyloses

Tyloses are oily secondary metabolites that contain phenolic substances and terpenoids (Kuroda 2001). In *Quercus macrocarpa* tyloses, a lignin content of ca. 28% has been measured (Obst et al. 1988). Tyloses are produced by the ray parenchyma and oxidize and polymerize in the vessel lumen in absence of water, thus in vessels that already are air-filled (Kuroda 2001). Cochard and Tyree (1990) studied tylose formation in ring-porous oaks (*Quercus alba* and *Q. rubra*) and discovered that early-wood vessels start getting filled with tyloses in the first winter after their formation, i.e. at the end of the growing season, to be fully blocked by tyloses by the next summer. Late-wood vessels on the other hand remained free of complete blockage for several years (Cochard and Tyree 1990). In *Q. robur* a wide protective layer, thought to play a role in tyloses formation, was only observed

inside axial and ray parenchyma of early- but not of late-wood (Kim and Daniel 2016b). Tylose-filled early-wood vessels after the growing season have been reported for several ring-porous species (Kitin and Funada 2016) and for the following oaks: *Quercus castaneaeifolia* (Safdari et al. 2008) and *Q. variabilis* (Kim and Hanna 2006; Pan et al. 2015). Tyloses were moreover commonly present in the wood of *Q. suber* (Sousa et al. 2009) and in the heartwood of *Q. robur* (Fromm et al. 2001; Sorz and Hietz 2006), being used as a potential criterion to define sapwood depth (Fromm et al. 2001; Sohara et al. 2012). Babos (1993) found tyloses in early-wood vessels to be increasing from stump (16 cm: 5.02%) upwards (12 m: 12.58%). Tylose formation can also be linked to wounding and pathogen infestation. In *Q. petraea* more sealed early-wood vessels were found in diseased tree trunks as compared to healthy ones (Babos 1993). Tyloses formation has also been observed in *Q. crispula* and *Q. serrata* trees after infestation by the fungus *Raffaelea* sp. (Kuroda 2001). Although supposed to be protective, the tyloses could not prevent the expansion of the fungus in the study of Kuroda (2001).

## 8.2.2 Tissue Properties

### 8.2.2.1 Parenchyma

Aggregate rays, i.e. large units of clustered ray parenchyma, are not unique to oaks but are uncommon in trees and they typically occur in Fagaceae (Carlquist 2001). This typical wood structure element can often be spotted with the naked eye in oak-made furniture or building parts. Together with the small rays and the axial parenchyma tissue, the large aggregated rays form the long-living (2–200 years) (Spicer and Holbrook 2007), elastic fraction of oak wood volumes, likely providing oxygen to the cambial zone and the bark (Spicer and Holbrook 2005) and defining the start of heartwood formation upon death (Spicer and Holbrook 2007). Internal water storage and water release has been linked to these elastic storage compartments, with the thickness of parenchyma cell walls playing an important role in the storage capacity (Jupa et al. 2016). However, in juvenile xylem from excised plant parts of five temperate tree species among which *Q. robur*, the importance of capillary compartments in water storage and release was much larger than that of parenchyma cells (Jupa et al. 2016). It is thus far unclear if this also stands for adult trees in natural conditions (Jupa et al. 2016). Jupa et al. (2016) compared the ring-porous *Q. robur* to diffuse-porous non-*Quercus* species and concluded that, contrary to the expectations, ring-porous wood does not seem to stand out in water storage and release capacity.

We employed the global dataset assembled by Morris et al. (2015) to examine existing data for radial, axial and radial plus axial parenchyma volumetric fractions for the genus *Quercus*. We found 24, 14 and 14 species of the genus *Quercus* for which data were available for the volumetric fractions of radial parenchyma, axial parenchyma and radial plus axial parenchyma, respectively. Given the small sample

size, it is impossible to draw any definitive conclusions about large-scale patterns. Overall, fractions of radial parenchyma in oaks varied between a minimum of 9% and a maximum of 34% (median of 21%), axial parenchyma varied between 11 and 26% (median of 21%) and total radial plus axial parenchyma varied between 24 and 46% (median of 42%). This compares with equivalent figures for the rest of the angiosperms of 2 and 68% (median of 17%), 0 and 74% (median of 11%) and 6 and 99% (median of 35%), respectively. Hence, the little available data do not show any unusual patterns for oaks relative to other angiosperms. The only discernible pattern in the dataset specifically for *Quercus* was that section *Lobatae* had significantly greater fractions of axial and radial plus axial parenchyma (but not radial parenchyma on its own) compared to *Quercus*, but given the limited sample size, caution needs to be exercised regarding the significance of this conclusion.

Few studies compare oak parenchyma content between organs or between trees growing under different environmental conditions, and if within-genus structural differences are observed, experimental proof for their possible functional significance is generally lacking. In saplings of *Q. robur*, *Q. petraea* and *Q. pubescens*, the density of non-ray parenchyma cells was slightly increased in drought-exposed individuals (Fonti et al. 2013). The authors suggest a role in embolism repair, more needed in dry conditions. Stokke and Manwiller (1994) found higher ray parenchyma content in roots, followed by branches and stems in *Quercus velutina*, proposing it to be related to the carbohydrate storage function of roots.

Besides in day-to-day tree physiology, xylem parenchyma also plays an important role in wood decay (e.g. Deflorio et al. 2009), wound reactions (Schmitt and Liese 1993, 1995) and pathogen infestations (Morris et al. 2016). The parenchyma tissue is often the place where trees are attacked by pathogens (or parasites) while at the same time parenchyma tissue is responsible for tyloses formation in reaction to infestation. Some example regarding oak species can be found in Kuroda (2001, *Q. serrata* and *Q. crispula*—ambrosia beetle *Platypus quercivorus*), Brummer et al. (2002, *Q. robur*—*Phytophthora quercina*), Miric and Popovic (2006, *Q. robur* and *Q. petraea*—fungus *Chondrostereum purpureum*), Medeira et al. (2012, *Q. suber*—*Phytophthora cinnamomi*), Ebadzad et al. (2015, *Q. ilex* and *Q. suber*—*P. cinnamomi*) and Cocolozzi et al. (2016, *Quercus germana*—*mistletoe Psittacanthus schiedeanus*).

### 8.2.2.2 Tracheids and Fibres

Wood fibres are known to provide mechanical support and are supposed to offer protection against vessel collapse (Metcalf and Chalk 1983; Hackett et al. 2001; Jacobsen et al. 2005; Jupa et al. 2016). They also play a role in the trees' water household (Jupa et al. 2016). Fibres as well as fibre-tracheids and tracheids can store water and thus contribute to the sapwood water storage and release capacity as has been proven for *Q. robur* by Jupa et al. (2016). This makes fibre and tracheid lumen size and pit characteristics important structural traits in tree hydraulics. Together with the vessel and parenchyma fraction, the fibre fraction defines the

density of a wood volume (Preston et al. 2006), mainly through the ratio of wall thickness to lumen size (Martínez-Cabrera et al. 2009; Ziemska et al. 2013). Fibre dimensions in oaks are found to vary with tree age, location within the tree and growth conditions (e.g. Lei et al. 1996; Leal et al. 2006; Yilmaz et al. 2008).

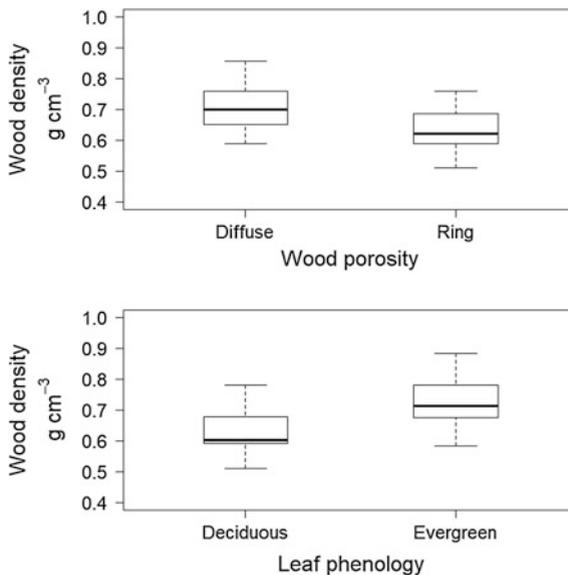
### 8.2.2.3 Wood Density

Wood density (*WD*, dry mass per fresh volume,  $\text{g cm}^{-3}$ ) is the basic measurement of the content of dry biomass within the green (or fresh) volume of a tree. It provides important ecological and physiological insights for foresters, ecologists and physiologists. Wood density varies between 0 and an upper limit of about  $1.5 \text{ g cm}^{-3}$ , which is the density of the wooden matrix alone (Whitehead and Jarvis 1981; Siau 1984). Different tree species can allocate different amount of carbon to produce their xylem structure, and an obvious trade-off emerges between the allocation to 'cheap' wood with lower construction costs to produce greater volumes of wood versus the allocation of 'expensive' wood with higher costs which might result in lower volumes being produced. Physiologically, across-species differences in wood density have been linked to differences in mechanical properties of wood (Young's modulus, stiffness, resistance to splitting, etc.), in hydraulic properties of the xylem (vulnerability to embolism, conductive efficiency, hydraulic capacitance), in defence against attacks by pathogens, in canopy architecture and in the ratio of leaf area to stem cross-sectional area (all of which are comprehensively reviewed by Chave et al. 2009). Ecologically, studies have often found negative relationships between wood density and either growth rates and/or likelihood of mortality in the field (e.g. Martínez-Vilalta et al. 2010). Therefore, it is important to examine general trends in wood density across the genus *Quercus* as a whole to determine whether broad patterns can be identified.

To do so, we employed existing compilations (Zanne et al. 2009; Chave et al. 2009) and enlarged that dataset by examining recent papers that collated wood density values for species not represented there (i.e. Cavender-Bares et al. 2004; Aiba and Nakashikuza 2009; Miles and Smith 2009; N avar 2009). Multiple entries for each species were averaged and all subsequent analyses were carried out using only species means. We recognise that significant limitations are present when wood density values are pooled across from a heterogeneous literature. Nonetheless, we agree with earlier authors (Chave et al. 2009; Zanne et al. 2010; and discussions therein) that these consolidation exercises have value in themselves and can provide novel insights.

Overall, we found wood density values for 99 oak species, with a relatively even spread across the three biomes (26 tropical, 50 temperate and 23 Mediterranean/semi-arid). The spread across sections of the genus was less even (19 in *Cyclobalanopsis*, 43 in *Quercus*, 29 in *Lobatae*, 5 in *Cerris*, 1 in both *Mesobalanus* and *Protobalanus*; we could not find any reference allowing classing *Quercus sideroxylo* within the genus). For the genus as a whole, wood density varied between 0.51 and  $0.88 \text{ g cm}^{-3}$ , with a median value of  $0.67 \text{ g cm}^{-3}$ .

The distribution of wood density values for the rest of the angiosperms has a minimum of 0.08, a maximum of 1.39 and a median of  $0.60 \text{ g cm}^{-3}$ , therefore suggesting that the genus *Quercus* occupies a fairly central position within the overall distribution of angiosperm wood density values, perhaps shifted towards values slightly above the mean. We log-transformed wood density values for all subsequent analyses to achieve normality of distribution. A very highly significant difference in  $\log(WD)$  was found according to phenology ( $P = 0.13 \text{ e}^{-8}$ ,  $N = 98$ ; Fig. 8.3), with evergreen species ( $N = 49$ ) having on average higher wood density values than deciduous ones ( $N = 49$  as well; back-transformed means of  $0.72$  versus  $0.62 \text{ g cm}^{-3}$ , respectively). A highly significant difference was also found with regard to wood porosity. Ring-porous species ( $N = 43$ ) had a significantly lower wood density compared to diffuse-porous ( $0.64$  vs.  $0.71 \text{ g cm}^{-3}$  respectively,  $P = 0.009$ ,  $N = 15$ , Fig. 8.3). Compared to section *Cerris* ( $WD = 0.73$ ), section *Quercus* and, especially *Lobatae* had significantly lower wood density ( $0.66$  and  $0.62 \text{ g cm}^{-3}$ ,  $P = 0.037$  and  $P = 0.002$ , respectively). Finally, a significant difference was also found among biomes ( $P = 0.0002$ ,  $N=99$ ). *Quercus* species from the temperate biome ( $WD = 0.65$ ) had significantly lower wood density compared to



**Fig. 8.3** Wood density box-and-whisker plots for two main grouping criteria, i.e. ring-porosity (diffuse- versus ring-porous) and leaf phenology (deciduous vs. evergreen). The dataset consisted of 98 *Quercus* species. Data were obtained from the primary literature and from existing compilations (see text for further details). In both cases, the differences between the two groups were highly significant ( $P = 0.009$  and  $P = 0.13\text{e}^{-8}$ , respectively). The thick line gives the median, the edges of the box are the lower and upper quartile, while the two whiskers extend up to 1.5 times the interquartile range from the top/bottom of the box to the furthest datum within that distance

those from the tropical ( $WD = 0.73$ ), but not the Mediterranean/semi-arid biomes ( $WD = 0.65$ ).

Overall, the data support the idea that evergreen sub-tropical species with diffuse-porous wood, especially of section *Cerris*, have higher wood density values than deciduous ring-porous oaks of the temperate and Mediterranean biomes, especially those of the *Lobatae* section. It is likely that these differences in wood density also map onto additional hydraulic features (see Sect. 8.3), such that variability in wood density across oak species better equip those with higher values for life under drier conditions.

### 8.3 Xylem Hydraulics

The xylem provides a low resistance pathway for water movement from the roots to the evaporation sites in leaves (Tyree and Zimmermann 2002). By supplying water to the leaves, it is a key element controlling plant water relations and stomatal responses, determining plant transpiration and assimilation rates (Sperry et al. 2017) and, ultimately, plant productivity and resistance to major stress factors such as freezing and droughts (Tyree and Sperry 1989; Brodribb 2009). The hydraulic properties of the xylem are usually summarized using two parameters, characterizing hydraulic efficiency and safety. Hydraulic efficiency corresponds to maximum transport capacity, and it is usually expressed as the sapwood-specific hydraulic conductivity under fully hydrated conditions ( $K_{S,max}$ ).  $K_{S,max}$  is quantified as the water flow through a wood segment per unit pressure gradient driving the flow, divided by the cross-sectional area of wood (Melcher et al. 2012). Hydraulic safety refers to the susceptibility to (drought-induced) embolism, as measured from vulnerability curves expressing how  $K_S$  declines as the water potential becomes more negative, indicating more stressful conditions. Several methods have been used to establish vulnerability curves, the most widely used being bench dehydration, air injection and centrifugation (Cochard et al. 2013). Vulnerability curves are frequently summarized using one single parameter: the xylem water potential inducing a 50% loss of hydraulic conductivity ( $\Psi_{50}$ ).

Here, we assembled a database of oak xylem hydraulic measurements starting with all oak entries in the Choat et al. (2012) functional xylem traits database, completed with Google Scholar searches of papers published after the compilation of the original dataset. Our analyses focus on  $K_{S,max}$  and  $\Psi_{50}$  values measured in stems, as data from other organs (roots and leaves) are scarce. In addition, we only considered direct hydraulic measures of  $K_{S,max}$  and  $\Psi_{50}$ ; that is, indirect measures based on conduit sizes (for  $K_{S,max}$ ) or acoustic emissions (for  $\Psi_{50}$ ) were discarded. Overall, we compiled data on stem  $K_{S,max}$  and  $\Psi_{50}$  for 41 and 32 oak species, respectively (Table 8.1), corresponding to a total of 89 individual vulnerability curves.

### 8.3.1 Measuring Xylem Hydraulic Properties in Oaks

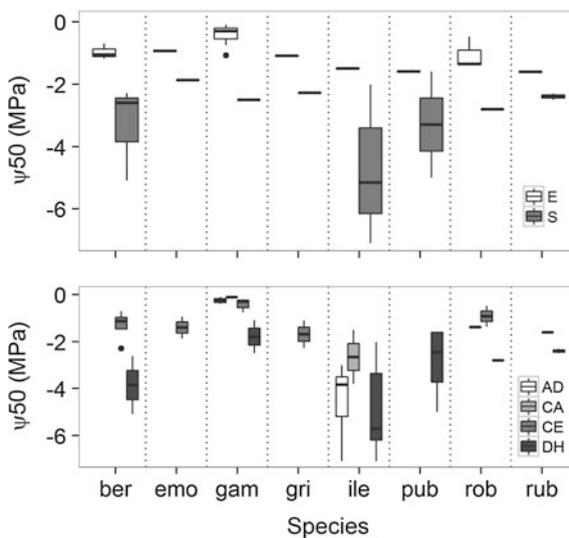
The measurement of xylem hydraulic properties in oaks is problematic for several reasons. Firstly, as already mentioned in the introduction, long vessels result in a substantial proportion of open vessels in measured wood segments. This leads to overestimations of both  $K_{S,max}$  (by not accounting for the resistance of pit membranes in open vessels; Melcher et al. 2012) and vulnerability to embolism (by exaggerating the percent loss of conductivity at a given pressure). The latter effect is not only caused by the overestimation of  $K_{S,max}$  but also because open, water-filled vessels are likely to be emptied immediately when subjected to any positive pressure, thus underestimating individual  $K_S$  measurements. Although this potential issue was recognized more than 20 years ago (Cochard and Tyree 1990; Sperry and Saliendra 1994; Martínez-Vilalta et al. 2002), it has received renewed attention in recent years (e.g. Cochard et al. 2010, 2013; Sperry et al. 2012; Hacke et al. 2015). The resulting artefact in vulnerability curves is supposed to affect mostly the air-injection and centrifugation techniques, and can be minimized by measuring  $K_{S,max}$  once open vessels have been emptied (through slight pressurization or gentle spinning; Sperry and Saliendra 1994; Alder et al. 1997). However, a limitation of this approach is that wider and longer vessels tend to be more vulnerable to embolism (Hargrave et al. 1994; Cai and Tyree 2010) and thus the population of vessels remaining once open conduits have been emptied may not be representative of the whole xylem. The bench dehydration technique is much less affected by these effects if sampled branches are longer than the longest vessels. However, even this technique, frequently considered the ‘gold standard’ to establish vulnerability curves, may be prone to related artefacts when measurement segments are cut under tension (Wheeler et al. 2013; Torres-Ruiz et al. 2015; but see Trifilò et al. 2014; Venturas et al. 2015).

A second issue, particularly relevant for ring-porous species and, therefore, many oaks, concerns the reference starting point for vulnerability curves. Initial  $K_{S,max}$  estimation is frequently done after flushing to remove any previously embolized vessels. However, flushing may refill conduits that were not functional in vivo, particularly in ring-porous species where only the most recent growth ring is functional. It has been recommended to work only with current-year shoots or exclude older growth rings (e.g. by gluing) before measurements are made in ring-porous species (Cochard et al. 2013). Another option is to sample in the wet season, before substantial embolism has developed, and consider the native  $K_S$  obtained under this conditions as a reasonable estimate of  $K_{S,max}$ .

The combination of the methodological issues described in the previous paragraphs is likely to have resulted in a huge variability in  $\Psi_{50}$  estimates for oaks, even within species. A large portion of this variability is associated to the shape of vulnerability curves: ‘sigmoidal’ curves generally having lower  $P_{50}$  (more resistant xylem) than ‘exponential’ curves (Cochard et al. 2013). Our data for oaks mirror the results obtained by Cochard et al. (2013) in that the vast majority of vulnerability curves obtained with the dehydration technique are reasonably sigmoidal in shape

(36 out of 39), whereas this is not the case for other methods (3 out of 35 for the static centrifuge, 1 out of 4 for the cavitron, 7 out of 11 for air-injection). Our database includes eight oak species (ring-porous and diffuse-porous) for which both shapes of curves have been measured. There is a striking difference in the estimated  $\Psi_{50}$  values between curve types for these species, with  $\Psi_{50}$  values being always more negative for sigmoidal curves, by as much as 1.8 MPa on average ( $P < 0.001$ ; Fig. 8.4). Differences between curve shapes correspond to differences among methods, with vulnerability curves obtained by dehydration generally showing more negative  $\Psi_{50}$  values (Fig. 8.4). Although  $K_{S,max}$  values were only reported for both curve types in four of the previous species, there was no consistent difference between curve types for this variable, suggesting that the differences in  $\Psi_{50}$  were not necessarily associated with biased  $K_{S,max}$  estimates.

While we share the view that exponential vulnerability curves are not necessarily wrong (Sperry et al. 2012), it seems hard to believe that the huge variability observed within species in the shape of vulnerability curves and associated  $\Psi_{50}$  values is real. In addition, some of the extreme  $\Psi_{50}$  values obtained from exponential vulnerability curves (11 curves with  $P_{50} > -0.5$  MPa, many for *Q. gambelii*) seem difficult to reconcile with the ecophysiology of the species, for which midday leaf water potentials are likely to be substantially lower than this value even under well-watered conditions (e.g. minimum water potential of  $-2.2$  MPa reported



**Fig. 8.4** Effect of vulnerability curve shape (upper panel: E, exponential; S, sigmoidal) and vulnerability curve method (lower panel: AD, air injection; CA, cavitron; CE, static centrifuge; DH, dehydration) on estimated vulnerability to embolism ( $\Psi_{50}$ ) for eight species in which both types of vulnerability curve shapes have been obtained. Species: ber, *Quercus berberidifolia*; emo, *Quercus emoryi*; gam, *Quercus gambelii*; gri, *Quercus grisea*; ile, *Quercus ilex*; pub, *Quercus pubescens*; rob, *Quercus robur*; rub, *Quercus rubra*

in Schwilk et al. 2016; but see Taneda and Sperry 2008). Direct imaging techniques such as X-ray computed microtomography (microCT) are promising to solve this vexing issue (Cochard et al. 2015), and have recently been applied to measure the vulnerability to embolism of *Q. robur*, a ring-porous oak (Choat et al. 2016). The  $\Psi_{50}$  obtained for living, intact *Q. robur* plants using microCT was  $-4.2$  MPa, much lower than the  $\Psi_{50}$  values obtained in the same study using the cavitron or static centrifuge techniques ( $-1.4$  and  $-0.5$  MPa, respectively), and also much lower than values reported in other studies using the centrifuge ( $-1.4$  MPa, Cochard et al. 1992) and even the bench dehydration method ( $-2.8$  MPa, Venturas et al. 2016). However, even microCT seems to give highly variable vulnerability curves within species (Nardini et al. 2017) and concerns have been raised about the correct interpretation of microCT results (Hacke et al. 2015). In addition, we note that as promising as the microCT technique is by being able to measure and visualize embolized conduits non-invasively, it does not directly measure the hydraulic impact of embolism. Studies modelling water transport in the xylem network show that conductivity is lost faster than the number of vessels (or the estimated theoretical conductivity in cross-sections) as water potential declines (Loepfe et al. 2007; Martínez-Vilalta et al. 2012), which could result in overestimating the resistance to embolism when using microCT (relative to purely hydraulic methods).

Before all these methodological issues are completely settled and standardized protocols are developed (Jansen et al. 2015), it can only be recommended that extreme care is taken at applying methodological protocols to measure hydraulic properties of oaks, and that different methodologies are compared whenever possible. In the following sections, we have taken an agnostic approach, using all data included in our database but always separating the  $\Psi_{50}$  values obtained from sigmoidal and exponential vulnerability curves.

### 8.3.2 An Overview of Oak Vulnerability to Embolism

The average stem vulnerability to embolism ( $\Psi_{50}$ ) for the 32 oak species included in our dataset is  $-2.5 \pm 0.3$  MPa (mean  $\pm$  SE), ranging from  $-0.5$  MPa for *Q. fusiformis* (McElrone et al. 2004) and *Quercus turbinella* (Hacke et al. 2006) to  $-7.0$  MPa for *Quercus coccifera* (Vilagrosa et al. 2003). This overall mean is close to the general average for angiosperms as reported in Choat et al. (2012) ( $-2.9 \pm 0.1$  MPa,  $N = 361$  species excluding oaks). However, if only sigmoidal vulnerability curves are included  $\Psi_{50}$  declines to  $-3.6 \pm 0.3$  MPa ( $N = 18$  species), which suggests that the oak genus may be a relatively resistant one within angiosperms. Root vulnerability to embolism has been only measured in seven oak species, with an average  $\Psi_{50}$  of  $-1.1 \pm 0.2$  MPa. Note, however, that the shape of all reported root vulnerability curves is exponential, except for two curves measured on *Q. ilex* by Limousin et al. (2010). When root and stem  $P_{50}$  were compared pairing the values by species and considering only studies in which both organs had

been measured (mixed-effects model), the difference between organs was only marginally significant ( $P = 0.05$ ), with root  $\Psi_{50}$  being more vulnerable by 0.4 MPa on average.

We studied how stem  $\Psi_{50}$  depends on taxonomic grouping, species biome, ring-porosity and leaf phenology. Due to limitations in sample size and close correspondence between some of these variables (e.g. most ring-porous oaks are deciduous) we assessed the effect of each variable separately, and thus our analyses are only meant to uncover broad associations. In all analyses the shape of the vulnerability curve (sigmoidal vs. exponential) was considered as a co-variate. Our results show that section *Cerris* has significantly lower (more resistant)  $\Psi_{50}$  than the *Quercus* or *Lobatae* sections ( $P = 0.04$  in both cases), whereas the only species in the section *Mesobalanus* (*Q. frainetto*) showed intermediate values. This is consistent with two of the three species in section *Cerris* being Mediterranean evergreen oaks adapted to dry habitats (*Q. coccifera* and *Q. suber*). No significant difference was observed among biomes, although Mediterranean/semi-arid species tended to have lower (more negative)  $\Psi_{50}$ . Ring-porous oaks were more vulnerable to embolism (modelled  $\Psi_{50} = -2.1 \pm 0.2$  MPa,  $N = 22$ ; compared to  $-3.2 \pm 0.4$  MPa for diffuse-porous species,  $N = 6$ ). Similar differences were observed between deciduous ( $-2.1 \pm 0.2$  MPa,  $N = 19$ ) and evergreen species ( $-2.8 \pm 0.3$  MPa,  $N = 13$ ), although in this case the effect was only marginally significant ( $P = 0.06$ ). Overall, the data are consistent with evergreen, diffuse-porous oaks occupying drier habitats being able to withstand more negative water potentials (being more drought tolerant) than species from wetter environments.

The results we showed are in line with earlier studies showing an association between oak species traits and their distribution along gradients of water availability (Monk et al. 1989; Villar-Salvador et al. 1997; Corcuera et al. 2002; Cavender-Bares et al. 2004), albeit some studies report contrasting associations for sympatric species (e.g. Knops and Koenig (1994) found that deciduous species were more drought tolerant).

Freezing-induced xylem embolism is an additional element that needs to be considered when relating xylem traits with oak distribution. The relatively wide xylem vessels of oaks, together with the well-known relationship between conduit size and vulnerability to freezing-induced embolism has been linked with the absence of oaks from cold climates prone to late frosts (Tyree and Cochard 1996). Within oaks, several studies have shown that deciduous species, which tend to have wider xylem vessels, are more vulnerable to freezing-induced embolism than evergreen species (Cavender-Bares and Holbrook 2001; Cavender-Bares et al. 2005), mimicking the patterns obtained for drought-induced embolism. Differences in freezing-induced embolism are also influenced by evolutionary lineage, with white oaks (section *Quercus*) being more vulnerable to freezing than live oaks (all evergreen) than red oaks (section *Lobatae*, including both evergreen and deciduous species) (Cavender-Bares and Holbrook 2001).

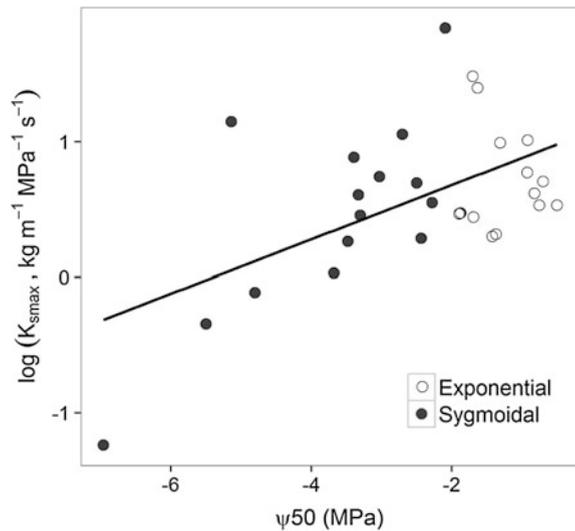
### 8.3.3 Hydraulic Conductivity and the Hydraulic Safety–Efficiency Trade-Off

The average stem  $K_{S,max}$  for the species included in our dataset is  $2.0 \pm 0.3 \text{ kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$  ( $N = 41$  species; values calculated after back-transformation from log-transformed data). The individual species values range from  $0.3 \text{ kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$  (*Q. coccifera*; Vilagrosa et al. 2003) to  $6.3 \text{ kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$  (*Quercus aliena*; Fan et al. 2011), and have a markedly right-skewed distribution. Consistent with the relatively large vessels of oaks (see Sect. 8.2.1), their average  $K_{S,max}$  is larger than the overall mean for angiosperms ( $1.5 \pm 0.1 \text{ kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$ ,  $N = 573$  species excluding oaks; data from Gleason et al. 2016). Root  $K_{S,max}$  is only available for seven species, with an overall average of  $7.1 \pm 0.9 \text{ kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$ , significantly higher than the value measured on stems for these same species ( $P = 0.004$ ; mixed-effects model of  $\log(K_{S,max})$ ).

As before, we also modelled  $\log(K_{S,max})$  as a function of taxonomic grouping, species biome, ring-porosity and leaf phenology. The results reveal significantly higher stem  $K_{S,max}$  for species in section *Lobatae* ( $N = 15$ ) than in section *Cerris* ( $N = 3$ ) ( $P = 0.01$ ), with *Quercus* species ( $N = 23$ ) showing intermediate values (no data available for section *Mesobalanus*). However, these results should be taken with care because only three representatives of the section *Cerris* were included (*Quercus acutissima*, *Q. coccifera* and *Q. suber*). Temperate species ( $N = 23$ ) have higher  $K_{S,max}$  than Mediterranean/semi-arid species ( $N = 14$ ) ( $P = 0.02$ ), with the four measured tropical species showing intermediate values. We also observed marginally higher  $K_{S,max}$  in ring-porous ( $N = 26$ ) relative to diffuse-porous species ( $N = 7$ ) ( $P = 0.08$ ). There was no difference in  $K_{S,max}$  between deciduous and evergreen species ( $N = 22$  and 19 species, respectively).

Data for oaks show clear indications of a hydraulic safety–efficiency trade-off, with a positive exponential relationship between  $\Psi_{50}$  and  $K_{S,max}$  (Fig. 8.5). This effect is highly significant ( $P = 0.001$ , overall  $R^2 = 0.42$  when the effect of vulnerability curve type is accounted for in the model,  $N = 29$  species) and particularly clear for species with sigmoidal vulnerability curves, whereas no relationship between  $\Psi_{50}$  and  $K_{S,max}$  was detected for species with exponential vulnerability curves (Fig. 8.5). This clear trade-off (at least when considering sigmoidal curves) contrasts with the poor relationship observed when all angiosperms are considered ( $R^2 = 0.05$  according to Gleason et al. 2016). We did not find evidence for the clustering of oak species in the low efficiency–low safety corner, contrary to what has been found in previous studies covering a wider range of species (Gleason et al. 2016).

**Fig. 8.5** Relationship between hydraulic safety ( $\Psi_{50}$ ) and efficiency (natural log of  $K_{S,max}$ ) for 29 oak species. Symbol colour indicates differences between vulnerability curve shapes (exponential vs. sigmoidal). The positive relationship between the two variables is highly significant ( $P = 0.001$ , overall  $R^2 = 0.42$  when the effect of vulnerability curve type is accounted for in the model)



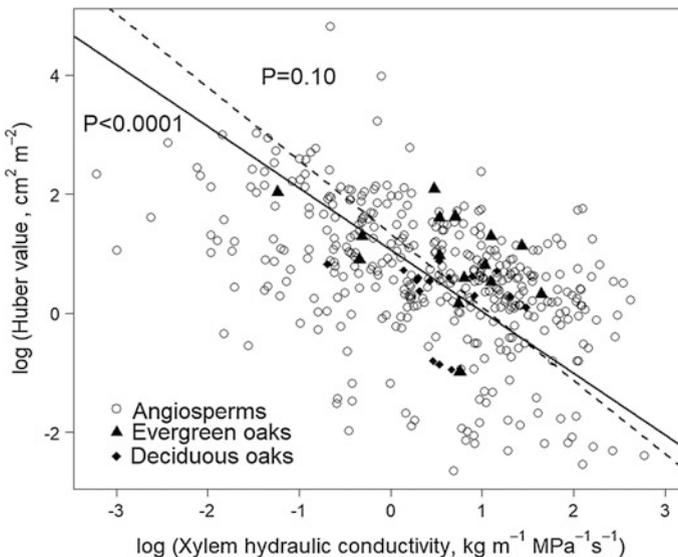
### 8.3.3.1 Huber Value and Relationships Between Allocation and Hydraulic Conductivity

The balance between water supply by the xylem and water demand by the canopy is mediated primarily by the relative allocation to these two tissues, a quantity variably named leaf-sapwood area ratio (leaf area divided by sapwood area) or Huber value ( $H_V$ , sapwood area divided by leaf area, Tyree and Ewers 1991). This allocation ratio is central to the interpretation of all measurements of plant hydraulics and water relations, because any estimate of the capacity of the xylem to efficiently conduct water per unit of sapwood area (i.e.  $K_{S,max}$ ) depends on the total cross-sectional area through which water flows and the area of the leaves distal to this section that transpires this water. In addition to the balance between water supply and demand, the Huber value affects also indirectly the balance between vulnerability to embolism  $\Psi_{50}$  and the minimum water potential  $\Psi_{min}$  that plants are willing to sustain, because at constant values of  $K_{S,max}$  and  $\Psi_{50}$ , greater allocation to leaf area relative to cross-sectional sapwood area will increase the demand on the xylem and the tension that the conductive system is expected to work under (e.g. Gleason et al. 2016). Several compensating mechanisms may allow plants to avoid or moderate the emerging trade-off between hydraulic safety and efficiency that was discussed in the previous section and which appears to be present also in *Quercus*. One important mechanism of compensation is the one involving the Huber value.

We considered therefore the relationships between the hydraulic traits mentioned above and Huber value. Consistent with a global relationship found elsewhere for

angiosperms (Rosas et al. *unpubl.*), a negative relationship was also found here between Huber value and maximum specific conductivity  $K_{S,max}$ , although the relationship for the genus *Quercus* was only marginally significant ( $P < 0.001$  for the global relationship and  $P = 0.10$  for the 31 oak species documented here, Fig. 8.6). Although only marginally significant, the negative relationship in oaks suggests the occurrence of compensation mechanisms between high allocation to supporting sapwood area and formation of a highly conductive xylem. Neither of the two slopes were significantly different from  $b = -1.00$  (i.e. 95% CI =  $-0.94$  to  $-1.13$  for all angiosperms and  $-0.83$  to  $-1.69$  for the oaks). Given that the leaf-specific conductivity  $K_L$  equals the product between  $K_{S,max}$  and  $H_V$ , a slope of  $-1.0$  is expected if all oak species had on average a constant  $K_L$  resulting in a perfect compensation. Obviously, more data across a larger sample of *Quercus* species are required to determine the degree of robustness of the relationship given here and therefore whether the genus *Quercus* also show compensation between water transport efficiency per unit of cross-sectional area and relative allocation between leaf area and sapwood area.

We then modelled  $H_V$  as a function of various grouping factors, as done in other sections above. Logarithmic transformation into  $\log(H_V)$  was required to achieve normality. A significantly lower stem  $H_V$  was found for species in section *Lobatae* ( $N = 13$ ) and marginally *Quercus* ( $N = 18$ ) than in section *Cerris* ( $P = 0.03$  and

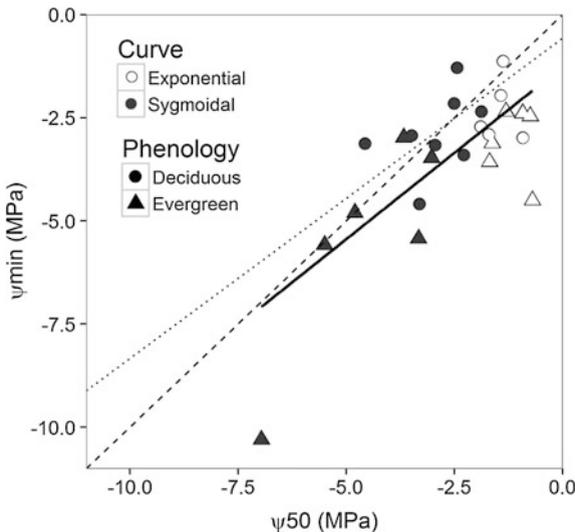


**Fig. 8.6** Relationship between the (natural) logarithm of Huber value and the (natural) logarithm of the maximum specific hydraulic conductivity for 375 non-oak angiosperms (Rosas et al. *unpubl.*) and for 31 *Quercus* species. Oak species are separated according to their phenology (evergreen vs. deciduous). The  $P$ -values refer to the significance of the negative relationships shown for the two datasets. Lines were fitted by standardised major axis regression

$P = 0.08$ , respectively), but only one representative of the section *Cerris* was present (*Q. coccifera*), so this relationship is very weak despite its level of significance. No difference was found between temperate species ( $N = 21$ ), tropical ( $N = 1$ ) and Mediterranean/semi-arid species ( $N = 10$ ). A significantly lower  $H_V$  ( $P = 0.006$ ) was found in ring-porous ( $N = 21$ ) than in diffuse-porous species ( $N = 3$ ), consistent with the (marginally) higher  $K_{S,max}$  found in ring-porous species (Sect. 8.3.3). Deciduous species ( $N = 17$ ) had significantly lower  $H_V$  ( $P = 0.013$ ) than evergreens ( $N = 15$ ).

### 8.3.3.2 Hydraulic Safety Margins and Drought Responses

Our data for oaks shows a strong coordination between the minimum leaf water potential measured for a given species ( $\Psi_{min}$ ) and its vulnerability to embolism ( $P_{50}$ ) ( $P < 0.001$ , overall  $R^2 = 0.67$  when the effect of vulnerability curve type is accounted for in the model,  $N = 25$  species) (Fig. 8.7), consistent with previous reports at community (e.g. Pockman and Sperry 2000; Martínez-Vilalta et al. 2002; Jacobsen et al. 2007) and global levels (Choat et al. 2012). Interestingly, the slope of this relationship for oaks appears to be similar to the global slope for angiosperms, whereas the intercept is smaller (Fig. 8.7), implying narrower hydraulic



**Fig. 8.7** Relationship between hydraulic safety ( $\Psi_{50}$ ) and minimum leaf water potential ( $\Psi_{min}$ ) for 25 oak species. Symbol colour indicates differences between vulnerability curve shapes (exponential vs. sigmoidal) and symbol shape distinguishes between leaf phenology (deciduous vs. evergreen). The overall linear fit to the data is shown as a continuous black line. The dotted line indicates the global fit for angiosperms from Choat et al. (2012), and the dashed line is the 1:1 relationship

safety margins (*HSM*) for oaks. The relatively narrow hydraulic safety margins for oaks are robust to differences in the shape of vulnerability curves. The slope of the relationship, however, must be interpreted with caution, as our data shows no significant relationship between  $\Psi_{min}$  and  $\Psi_{50}$  for exponential curves, whereas the slope of the relationship for sigmoidal curves is highly significant and steeper (1.3, 95% confidence intervals: 0.8–1.8) than the overall slope for angiosperms (0.8; Choat et al. 2012). A slope >1 implies that the hydraulic safety margin is narrower for species having lower  $\Psi_{50}$  or experiencing more negative  $\Psi_{min}$ .

The relationship between  $\Psi_{min}$  and  $\Psi_{50}$  was similar for temperate and Mediterranean/semi-arid oak species, even though the latter species tended to have lower  $\Psi_{min}$  and  $\Psi_{50}$  and, thus, be located towards the bottom-left corner of the graph (not shown). On the other hand, the compiled oak data show a marginal effect of leaf phenology on the relationship between  $\Psi_{min}$  and  $\Psi_{50}$  ( $P = 0.071$ ), with both species types having similar slopes but evergreen species having narrower hydraulic safety margins (0.9 MPa on average) (Fig. 8.7). This result and particularly the fact that hydraulic safety margins are nearly always negative for evergreens (regardless of the shape of the vulnerability curve) is rather counter-intuitive. Note, however, that these narrower hydraulic safety margins for evergreens do not arise from greater vulnerability to embolism (rather the opposite, as we have seen before) but from lower minimum water potentials at a given xylem vulnerability. This pattern suggests either a more risk-averse strategy for deciduous species or adaptations in other parts of the soil-plant-atmosphere-continuum allowing evergreen species to sustain proportionally greater xylem stress. These adaptations may include a higher Huber value and, thus, higher leaf-specific hydraulic conductivity  $K_L$  in evergreens (e.g. Cavender-Bares and Holbrook 2001) or systematic differences in stomatal or rooting behaviour. As shown in the previous section, across 32 species a trend of increased Huber value in evergreen species was indeed found, supporting the explanation above.

## 8.4 Concluding Remarks

Oak species are very diverse in their ecology and life history, and this diversity is also reflected in their xylem anatomy and function. In this chapter, we have reviewed the main aspects of the xylem structural properties at vessel and tissue level, as well as the hydraulics of oaks. We have done so by combining qualitative reviews from the primary literature when data availability is relatively low or disperse, with quantitative syntheses for the variables for which consolidated databases already existed, some of which have been expanded substantially. We admit that by working with heterogeneous data sources generally covering a small percentage of overall oak diversity, as well as by ignoring intra-specific variability (our analyses are focused at the species level), we are making important assumptions that may limit our capacity to draw general conclusions. Despite these caveats, some general patterns emerged that are summarized in the following paragraphs.

Some of these patterns appeared to be specific for oaks and, in our opinion, merit further investigation.

From a wood anatomical perspective, oaks are characterized by relatively low vessel density and medium to high vessel sizes, which result in low lumen fractions and, everything else being equal, high mechanical strength. Although hydraulic conductivity is highly sensitive to the lumen fraction (Zanne et al. 2010), oaks do not seem to pay an important price in terms of transport efficiency, as they are characterized by relatively high sapwood-specific hydraulic conductivity ( $K_{S,max}$ ) relative to other angiosperms. This is likely related to the presence of long vessels in many oak species and it might be related to relatively high permeability of their inter-vessel pit connections. Long vessels contribute towards increasing the connectivity of the xylem network (sensu Loepfe et al. 2007). However, the high percentage of solitary vessels, characteristic of oaks, has the opposite influence. The net effect of these two patterns on the connectivity of the xylem network remains to be elucidated as is the role of tracheids in conduction. High  $K_{S,max}$  in oaks tends to be associated with high investment in leaf area per unit of cross-sectional sapwood area (low Huber value), similar to the pattern observed when all angiosperms are considered.

Oak vulnerability to embolism ( $\Psi_{50}$ ) appears to be extremely variable, and its measurement is plagued with methodological issues that limit our capacity to draw general conclusions. Many published values appear hard to recognize with the known ecology of the species, but even when all data were pooled together (while accounting for methodological effects in models) some clear patterns emerged. Firstly, a strong safety–efficiency trade-off between  $K_{S,max}$  and  $\Psi_{50}$  was observed for oaks, much clearer than the pattern reported when all angiosperm species were considered. Secondly, oaks followed a similar relationship between  $\Psi_{50}$  and the leaf minimum water potential experienced in the field ( $\Psi_{min}$ ) to the one reported for angiosperms (Choat et al. 2012) but with even narrower hydraulic safety margins. Importantly, this pattern held even when only sigmoidal vulnerability curves were considered. This result has important implications in the context of increased frequency and intensity of extreme drought events under ongoing climate change, which has already affected several oak species worldwide (see Chapter on drought-induced oak decline in this book). At the same time, however, many oak species show high resprouting capacity, frequently resulting in fast recovery after canopy dieback (e.g. Lloret et al. 2004).

With regards to patterns of variation within the *Quercus* genus, we report consistent differences among taxonomic groups, particularly between sections *Quercus* and *Lobatae*, on the one hand, and *Cerris*, on the other. The former sections had smaller but more numerous vessels, lower wood density, more vulnerable xylem and generally higher conductivity ( $K_{S,max}$ ). These differences do not necessarily agree with expected relationships between wood anatomy and function, as high densities of smaller vessels are normally interpreted as an indicator of high resistance to embolism (e.g. Pfautsch et al. 2016), illustrating the complexities of making this type of generalizations even when comparing phylogenetically close species within the same genus. These consistent differences among taxonomic

groups were partially reflected in broad scale biogeographic patterns, with temperate oak species having higher conduit density and lower wood density than tropical species. Temperate oak species had also higher conductivity ( $K_{S,max}$ ) than Mediterranean/semi-arid species, and tended to be more vulnerable to embolism, consistent with the expectations based on differential drought exposure in these different biomes.

Ring-porosity and leaf phenology are highly associated in oaks, with most evergreen species being diffuse-porous and most deciduous species being ring-porous. In agreement with this, we frequently observed consistent patterns when assessing the effects of these two variables. Although we did not observe clear patterns in vessel anatomy between these groups, probably reflecting limited sample size and methodological heterogeneity, we found clear differences in wood density and hydraulic traits. Ring-porous (deciduous) species had lower wood density, higher hydraulic conductivity ( $K_{S,max}$ ) and were more vulnerable to xylem embolism, consistent with expectations based on the fact that these species do not generally occupy dry environments. How these patterns relate with other stress factors (e.g. low temperatures) and with overall plant resource-use strategies is an important question that merits further investigation.

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