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Assessing inter- and intraspecific variability of xylem vulnerability to embolism in oaks

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Abstract

The genus *Quercus* comprises important species in forestry not only for their productive value but also for their ability to withstand drought. Hence an evaluation of inter- and intraspecific variation in drought tolerance is important for selecting the best adapted species and provenances for future afforestation. The presence of long vessels makes it difficult to assess xylem vulnerability to embolism in oak. Thanks to the development of an in situ flow centrifuge equipped with a large rotor, we quantified (i) the between species variability of embolism resistance in four native and two exotic species of oaks in Europe and (ii) the within species variability in *Quercus petraea*. Embolism resistance varied significantly among species, with the pressure inducing 50% loss of hydraulic conductivity (P_{50}) ranging between - 7.0 and -4.2 MPa. Species native to the Mediterranean region were more resistant than pan-European species. In contrast, intraspecific variability in embolism resistance in *Q. petraea* was low within provenances and null among provenances. A positive correlation between P_{50} and vessel diameter among the six oak species indicates that the more embolism resistant species had narrower xylem vessels. However, this tradeoff between hydraulic efficiency and safety was not observed between *Q. petraea* provenances.

Keywords

plant hydraulics; xylem embolism; drought resistance; climate change; oaks

Introduction

Climate change projections predict a significant effect on the growth and survival of forests (Reyer *et al.*, 2014) but the impact on growth rate is species specific. While species in

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northern latitudes are expected to benefit from a warmer climate (Talhelm *et al.*, 2014), species growing under temperate or more southern latitudes will be negatively affected (Reyer *et al.*, 2014). With the predicted climate change scenario (IPCC 2014), mean annual temperatures are expected to increase and patterns and frequency of rainfall may change considerably. This will probably result in more frequent summer drought events in most parts of Europe. Such drought events will have important implications for vegetation distribution and dynamics as seen from the evidence of drought-induced forest dieback in various parts of the world (Allen *et al.*, 2010; Cailleret *et al.*, 2017) including Europe (Bréda *et al.*, 2006; Anderegg *et al.*, 2016). Understanding the mechanisms leading to such mortality events as well as the capacity of the trees to cope with drought is therefore crucial in predicting the ecological consequences of ongoing climate change.

For trees, drought survival relies on their ability to control the loss of water during an extreme event (McDowell *et al.*, 2008). Drought induced dieback in forest trees is mainly a result of xylem hydraulic failure (Anderegg *et al.*, 2013; Anderegg *et al.*, 2016) caused by the formation of air bubbles (embolism) in the xylem conduits which disrupt the water transport from the roots to the leaves (Tyree & Zimmermann, 2002). Vulnerability to embolism (P_{50} , water potential at which 50% of hydraulic conductivity is lost) and the hydraulic safety margin (difference between P_{50} and minimum xylem water potential under natural conditions) are key physiological traits linked to tree mortality under severe drought (Brodribb & Cochard, 2009; Brodribb *et al.*, 2010; Barigah *et al.*, 2013; Meinzer *et al.*, 2009; Torres-Ruiz *et al.*, 2017a; Urli *et al.*, 2013). A recent survey on 226 tree species across the world found that more than 30% of the species had narrow hydraulic safety margins, making them susceptible to drought (Choat *et al.*, 2012). Vulnerability curves evaluate the loss of xylem conductance as the xylem pressure decreases thereby providing a valuable method to assess the drought resistance (Cochard *et al.*, 2013). This allows the estimation of hydraulic traits such as P_{50} which is commonly used to characterize drought tolerance at local and global scales as well as across species (Maherali *et al.*, 2004; Trueba *et al.*, 2017).

Among-species variation in resistance to embolism was earlier reported in conifers (Bouche *et al.*, 2014; Delzon *et al.*, 2010). It is also reported that within-species variation can be considerably less than the among-species variation (David-Schwartz *et al.*, 2016; Lamy *et al.*, 2014). Intraspecific variability in resistance to embolism in conifers can be of larger magnitude than intraspecific variability in angiosperms (Anderegg, 2015) although such studies are very limited in number. The issue is complicated in the long-vesselled angiosperm species, because the commonly used methods to construct vulnerability curves can lead to biased results (Torres-Ruiz *et al.* 2014; 2017a; Cochard *et al.* 2013; Ennajeh *et al.* 2011). This is the case for ring porous species such as oak for which maximum vessel length above 70cm has been typically reported (Cochard and Tyree 1990; Martinez-Vilalta *et al.* 2002; Jacobsen *et al.* 2007). The vulnerability to embolism may be overestimated in previous studies due to both the so called “open-vessel” (Cochard *et al.* 2013; Torres-Ruiz *et al.* 2014 and 2017a) and “cutting” (Wheeler *et al.*, 2013; Torres-Ruiz *et al.*, 2015) artefacts. The overestimations are especially evident by using centrifuge techniques as the *in situ* flow centrifuge (Cavitron) in which the samples are spun to gradually expose them to decreasing xylem pressures while monitoring the loss of hydraulic conductivity (Cochard, 2005). These

artefacts have therefore questioned the reliability of previous results reported on resistance to embolism of long-vesselled species, complicating the proper evaluation of their function.

The genus *Quercus* comprises approx. 415 reported species across America, Asia, North Africa and Europe (Oh and Manos, 2008; Hubert *et al.*, 2014). In Europe, *Quercus petraea* and *Q. robur* are the two widely distributed species extending from Spain to Scandinavia (Ducousso & Bordacs, 2004). Their pan European distributions suggest their high ability to adapt to very diverse growing conditions and, therefore their suitability for future climates (Epron & Dreyer, 1993; Arend *et al.*, 2011; Eaton *et al.*, 2016). The evergreen oak species, *Q. ilex* and *Q. suber* are two of the most common species of the Mediterranean forests and they have demonstrated capacities to withstand drought (David *et al.*, 2007). While drought-induced mortality events are reported for *Q. robur* (Urli *et al.*, 2014) and *Q. petraea* (Cochard *et al.*, 1992), other *Quercus* species have shown a high tolerance to drought (Baquedano & Castillo, 2007) including capacity to recover their canopy after a drought event (Lloret *et al.*, 2004). Such different species responses to drought could be due to inherent differences in morphological and physiological traits of adaptive significance and/or phenotypic plasticity. However, an accurate quantification of the interspecific variation in resistance to embolism within the genus *Quercus* is still lacking. Moreover, experimental evidence of the adaptive significance of the resistance to embolism is also absent in oaks. Therefore, an evaluation of the species genetic variation in resistance to embolism is crucial in order to anticipate the response of major European *Quercus* species to climate change.

The aim of the present study was to assess inter- and intraspecific variability in resistance to embolism in the oak genus. First, we quantified the resistance to embolism in six *Quercus* species widely distributed in Europe by using a newly developed prototype of Cavitron equipped with a 1m-diameter rotor. This reduces the amount of cut-open vessel in the xylem samples and, therefore, prevents artefactual losses in hydraulic conductance by avoiding the ‘open-vessel’ artefact. Secondly we investigated the amount of genetic differentiation among provenances in resistance to embolism, by sampling four *Q. petraea* provenances growing in a common garden and originating from temperate and Mediterranean latitudes in Europe. Results are expected to provide relevant information not only about the ability of the different *Quercus* species to withstand the adverse effects of drought events, but also show its capacity to adapt to the new climate conditions imposed by the human-induced climate change.

Materials and Methods

Interspecific variation in xylem vulnerability to embolism for 6 oak species

Vulnerability to embolism was evaluated in six oak species: four were native European species (*Quercus petraea*, *Q. ilex*, *Q. robur* and *Q. suber*) and two were exotic species introduced from North America (*Q. palustris* and *Q. rubra*). Their native distribution range is given in Fig.S1 in supplementary information. For each species, two branches were collected from 5 to 16 healthy mature trees growing in Southern France (INRA and University of Bordeaux campus). All branches were a minimum of two meters long ranging between 18 and 20 mm in diameter, collected in the early morning using a pole pruner from the sunny side of the crown. Sampling was made within a period of six weeks in summer 2015. Once

collected, transpiration losses from the branches were prevented by removing the leaves immediately after sampling and wrapping them in moist paper to keep them wet during their transportation to the lab. Once in the lab, branches were stored at 3°C until resistance to embolism was assessed (within three weeks of sampling).

Intraspecific variation in xylem vulnerability to embolism for *Quercus petraea*

For evaluating the genetic differentiation in vulnerability to embolism among *Quercus petraea* (sessile oak) provenances, we used a common garden experiment planted in 1986 and 1987 in the Forêt Domaniale de Sillégny (France) which contains in total 107 sessile oak provenances. The initial density of plantation was 1904 individuals per hectare (spacing 3 m × 1.75 m) with each provenance replicated from ten to fifteen times having 24 trees per replicate. Four provenances selected for the present study; Grésigne (Southeastern France), Killarney (Southern Ireland), Vachères (Southwestern France) and Göhrde (Northern Germany) (Fig. 1, Table 1) represent different climatic regions, ranging from dry Mediterranean region in France to continental temperate climate in Germany. For each provenance, the aridity index (AI) was calculated as;

$$AI = MAP/MAE$$

where MAP = Mean Annual Precipitation and MAE = Mean Annual Potential Evapotranspiration.

We collected 12 to 15 trees per provenance in the common garden experiment. Trees of each provenance were sampled in five replications. Trees of the common garden were on average 10 m tall, and 2m long branches were cut from upper part of the tree. Branches were wrapped in wet paper before being immediately transported to the lab and then processed as branches collected for the species comparison.

Vulnerability curves

Vulnerability to drought-induced embolism was determined at the Caviplace (University of Bordeaux, Talence, France; <http://sylvain-delzon.com/caviplace>) with the Cavitron technique (Cochard 2002; Cochard 2005). To prevent artefactual losses in hydraulic conductance due to the presence of open vessels in the samples (Pivovarovoff *et al.*, 2016; Torres-Ruiz *et al* 2017a), branches were recut under water to a 1m-long length, debarked at both ends and then installed in a large cavitron equipped with a 1m-diameter custom-built honeycomb rotor (DGMeca, Gradignan, France). Several samples per species were used to test the presence of open vessels by air injection at 2 bars and none of the studied species presented open vessels in 1 m long branches. Centrifugal force was used to establish negative pressure in the xylem (P_i) and to provoke water stress-induced cavitation. Samples were spun for two minutes at a given speed to decrease the xylem pressure progressively at its center from -0.8 MPa to -10.5 MPa (those pressures correspond to centrifugation rotation from 764 rpm to 2768 rpm respectively). Samples were three to five years old with a diameter varying from 10.3 to 12.2 mm. As this technique enables measuring the hydraulic conductance of the samples under negative pressure, the vulnerability curves were generated by plotting the percentage loss of hydraulic conductivity (PLC) against the different target pressures applied. For each branch,

the relationship between PLC and the xylem pressure induced by centrifugation was fitted with the following sigmoidal equation (e.g., Pammenter & Vander Willigen 1998):

$$PLC = \frac{100}{\left(1 + \exp\left(\frac{S}{25(P_i - P_{50})}\right)\right)}$$

where P_{50} (MPa) is the xylem pressure inducing a 50% loss of conductivity and S (% MPa⁻¹) is the slope of the vulnerability curve at the inflexion point. Mean values of embolism vulnerability parameters (P_{50} and S) correspond to the average values of 5 to 16 samples per species. The P_{50} value shows the ability of the branch to maintain its conductance at negative pressures and is commonly used as a proxy for the tree drought resistance. The lower the P_{50} value, the more drought tolerant the species or the provenance (Delzon 2015).

Anatomical traits

For each oak species and *Q. petraea* provenance, 30µm to 50µm sections were cut from 5 to 10 of the branches used for vulnerability curve measurements using a sliding microtome (GLS1-microtome, Schenkung Dapples, Switzerland). After sectioning, they were bleached, rinsed with milliQ water and stained with a 1:2 mixture of safranin (0.5% in 50% ethanol, Safranin _ Fisher scientific _ General purpose grade) and alcian blue (1% in water, Alcian Blue 8GX _ Alfa Aesar). After this, sections were washed with milliQ water and five times with 50, 70 and 96% ethanol. Slides of the sections were mounted with Euparal (Euparal 100g _ ROTH) and left to fix at room temperature. After one or two days, slides were placed in the oven at 60°C and the best ones were selected to be scanned. The entire transverse section of each sample was digitized at 20X magnification using a desktop single slide scanner (Nanozoomer 2.0 HT, Hamamatsu). The pictures from the scanner were later processed and analyzed ring by ring to quantify several anatomical traits such as vessel diameter in µm (d), vessel density in n mm⁻² (VD), hydraulically weighted vessel diameter in µm (d_h , that is the sum of all conduit diameters ($\sum d^5$) divided by the total number of conduits ($\sum d^4$; Sperry *et al.*, 1994) and relative theoretical conductivity in kg m⁻¹ MPa⁻¹ s⁻¹ (K_s). The average of each trait was calculated for the whole cross section (d , d_h , VD , K_s) and for the last ring (d_{ring} , d_{h_ring} , VD_{ring} , K_{s_ring}).

Statistical Analysis

Before the analyses, we confirmed the normal distribution of values for all variables measured (Shapiro-Wilk test; $\alpha = 0.05$). To compare vulnerability to embolism between oak species and provenances of *Q. petraea*, we used one-way analyses of variance with post hoc Tukey's honest significant difference using 95% confidence intervals to compare hydraulic traits values (P_{50} , P_{12} , P_{88} , S) across species and provenances. Coefficients of variations (CV_{intra}) were estimated within each species and provenance. For *Q. petraea*, the between-provenance variability (CV_{inter}) was calculated from the between-provenance standard deviation and the overall mean value. Pearson's correlation analysis was used to test for relationships between hydraulic and anatomical traits between and within species. All analyses were performed in SAS 9.4 (SAS Institute, Cary NC).

Results

Interspecific variation among oak species

For each species, vulnerability curves showed similar sigmoid shapes (Fig. 2, Fig.3) with the air-entry (P_{12}) ranging from -4.93 in *Q. ilex* to -2.14 in *Q. rubra* (Table 2). Values of P_{50} significantly varied between species ($F = 39.12$; $P < 0.0001$), ranging from -7.13 in *Q. ilex* to -4.43 in *Q. rubra* (Table 2). Similar significant variation in P_{12} ($F = 7.94$; $P < 0.0001$), and P_{88} ($F = 40.50$; $P < 0.0001$) was observed across species with *Q. ilex* and *Q. rubra* at the extremes of the range. The vulnerability curve slope, S ($F = 2.15$; $P < 0.07$) was not significantly different among the species. The species with lowest P_{50} and hence more resistant to xylem embolism were the two Mediterranean species *Q. ilex* and *Q. suber* and the North American species *Q. palustris* whereas the more vulnerable species were *Q. rubra*, *Q. petraea* and *Q. robur* (Fig. 3). The coefficient of variation in P_{50} (CV) is low and varied from 5.17% in *Q. robur* to 13.71% in *Q. rubra* (Table 2).

Intraspecific variation in *Q. petraea*

In *Q. petraea*, all provenances exhibited sigmoidal vulnerability curves (Fig. 4) and no significant differences were found for any embolism resistance trait among the four provenances (Fig. 4; Table 3, Fig. S2). The maximum difference in P_{50} was only 0.34 MPa (Table 3) and was not significantly different among the provenances ($F = 1.53$; $P = 0.22$). Similarly, the maximum differences between provenances were only 0.62 and 0.26 MPa, for P_{12} and P_{88} , respectively (Table 3) and no significant differences were found for those traits between provenances. The vulnerability curve slope, S ($F = 1.90$; $P = 0.14$) was also not significantly different among the provenances (Table 3). The P_{50} values measured for a given provenance showed a relatively moderate variability with average CV_{intra} for provenances of 10.5% (Table 3). However this within-provenance variability was much larger than the inter provenance variability ($CV_{inter} = 3.5\%$).

Correlation between P_{50} and xylem anatomical traits

Significant differences were found between species for d_{ring} ($F = 3.84$; $P = 0.009$), d_h ($F = 4.52$; $P = 0.004$), d_{h_ring} ($F = 9.61$; $P < 0.0001$), K_s ($F = 2.57$; $P = 0.05$) and K_{s_ring} ($F = 4.36$; $P = 0.004$) indicating that Mediterranean species (*Q. ilex* and *Q. suber*) have smaller vessels than the others. The other analyzed anatomical traits did not show any significant differences between species. Among the six oak species, P_{50} was positively correlated with d_{ring} , d_{h_ring} , d_h and K_{s_ring} (Table 4, Fig. 5). These correlation were calculated at the individual tree level over all species, but the distribution of the species mean values on the regression diagram (Fig.5) indicate that the correlation is mostly driven by the species effect: the more resistant to embolism the species, the narrower the vessels. There were no significant correlations between hydraulic traits and vessel density (VD and VD_{ring}).

No significant differences of anatomical traits were observed between provenances within *Q. petraea* except for VD ($F = 4.20$; $P = 0.01$), (Table S3 in supplementary information). However, P_{50} was negatively correlated with d , d_h , d_{h_ring} as well as K_s (Table 4, Fig. 5): the more resistant to embolism the individual, the larger the vessels. As there were no significant differences between provenances, we computed correlation among traits at the

within provenance level (individual tree level) by merging the data of all provenances (Fig. 5). Here the correlations are mostly driven by the individual tree effect, rather than by the provenance effect (Fig. 5). There were no significant correlations between hydraulic traits and vessel density (VD and VD_{ring}). Quite strikingly regression coefficients between anatomical and hydraulic traits were of opposite signs at the species and provenance level (Table 4).

Discussion

Oak species show large interspecific variation in embolism resistance

Large variation in resistance to embolism was found among the six oak species studied, with a higher resistance in those occurring in the Mediterranean biome, such as *Q. ilex*, than those occurring in temperate cooler climates. Previous studies have shown that resistance to xylem embolism is a key trait allowing trees to survive in an extreme water scarcity environment (Urli *et al.*, 2013; Brodribb and Cochard 2009, Anderegg *et al.* 2015). Such variation among species was earlier observed among angiosperms where embolism resistance was negatively correlated with mean annual precipitation of the species distribution range (Maherali *et al.*, 2004; Choat *et al.*, 2012). In addition, Mediterranean species are well-known for being more resistant to embolism than temperate species (Urli *et al.*, 2014; Gimeno *et al.*, 2009). Indeed, we found the temperate species *Q. rubra* as being the most vulnerable to embolism, even more vulnerable than its European counterparts as previously reported by Cochard *et al.*, (1992). A similar study by Cochard *et al.* (1992) compared three native European oak species. According to their results, *Q. robur* was more vulnerable to embolism (P_{50} of -2.5 MPa) than *Q. petraea* and *Q. pubescens* (P_{50} of -3.3 MPa for both species). Those values are substantially less negative from those obtained in this study but they still show a similar trend among the species. Indeed large discrepancies in P_{50} values for a given species have been previously reported mainly due to use of different methods for determining their vulnerability to embolism (see Cochard *et al.* 2013). For instance, Martin St-Paul *et al.* (2014) showed that the P_{50} values in *Q. ilex* varied anywhere between -2 to -8.2 MPa due to the “open-vessel artefact” involved in the traditional methods for obtaining vulnerability curves to cavitation. Also, Venturas *et al.* 2016 showed very different results in *Q. robur* with a P_{50} of -1.4 MPa when vulnerability curves were measured using single vessel air injection technique. To avoid any artefactual results due to presence of open vessel in the samples, a large rotor (1 m in diameter) was used in this study to determine the resistance to embolism for the six *Quercus* species. Thus, we obtained S-shaped curves for each species, and *Quercus robur* showed a similar P_{50} value (-4.7 MPa) as reported by Choat *et al.* (2015) using the reference microCT technique (-4.2 MPa). This suggests that, when using large diameter rotor (1m), the centrifuge technique reports accurate P_{50} values for long-vesseled species as *Q. robur* while it is well known that standard rotors (0.27 m in diameter or less) overestimate their vulnerability to embolism thus supporting open vessel artifact hypothesis (Choat *et al.*, 2010; Cochard *et al.*, 2010; McElrone *et al.*, 2012; Martin-StPaul *et al.*, 2014; Torres-Ruiz *et al.*, 2014,2017). Caution is still advised when applying this technique to species with vessel lengths that exceed the diameter of the rotor used in centrifuge methods.

Lack of genetic differentiation among provenances in resistance to xylem embolism

Within *Q. petraea*, we found no significant genetic differentiation in resistance to embolism among different provenances originating from different climatic regimes. Exploring the genetics behind plant hydraulics is still a developing area of research (Venturas *et al.*, 2017) and very few studies have been successful in quantifying intraspecific variation in resistance to embolism in angiosperms so far. Lack of genetic differentiation in embolism resistance between provenances for P_{50} has been already reported for conifer species (Corcuera *et al.* 2011; Lamy *et al.* 2011; Sáenz-Romero *et al.* 2013). For example, Lamy *et al.* (2011) found a very narrow range in embolism resistance (0.2 MPa) for six *Pinus pinaster* populations grown in a provenance trial. Narrow ranges of xylem embolism resistance variability between populations of the same tree species suggest a highly canalized response driven by uniform selection of this trait (Lamy *et al.* 2011; 2014). Studies on *Fagus sylvatica* provenance trials have also reported low genetic differentiation among populations both in hydraulic as well as anatomical traits (Wortemann *et al.*, 2011; Hajek *et al.*, 2016). Likewise our *Q. petraea* provenances from different climates and with different evolutionary histories (Petit *et al.* 2002) shared similar embolism resistance value, suggesting an evolutionary process behind the lack of variability of this trait. Consequently, this low genetic differentiation within species limits the evolution of species through divergent selection especially in its southern margin of distribution range (Kremer *et al.*, 2013).

In our study, the range of within-provenance differentiation is much larger (Table 3) than the range of the among provenance variation (CV_{inter} 3.5%). Interestingly, this moderate genetic differentiation within provenances was maintained even while no genetic differentiation was observed between provenances. *Q. petraea* is a wind pollinated species and has previously been found to be predominantly outcrossing with random mating (Bacilieri *et al.* 1996). High levels of gene flow among populations across landscapes have also been reported in the species (Gerber *et al.* 2014). Sessile oak usually occur in large populations. The presence of moderate genetic differentiation within populations and the absence of genetic differentiation among populations as seen from our results suggest that selection can happen within these populations for adaptive traits (Scotti *et al.* 2016). Selected genotypes can be maintained within these populations even if there is a high gene flow among these populations (Aitken and Bemmels, 2016; Lowe *et al.* 2015; Kremer *et al.* 2012). By working on a common garden trial with provenances coming from contrasting climatic conditions, we were able to quantify genetic differentiation but not the environmental effects. A more elaborate sampling of branches from trees growing in more diverse growing conditions is required to draw more conclusions regarding the phenotypic plasticity of embolism resistance. The need for testing provenances from extreme sites is also recommended in future in order to test whether marginal populations have evolved more embolism resistant xylem.

Relationship between embolism resistance and xylem anatomical traits

The positive correlation observed between P_{50} and vessel diameter indicates that the more embolism resistant species possess narrower xylem vessels (Table 4, Fig. 5). This agrees with former studies in other angiosperms showing greater vulnerabilities to embolism for those species with wider vessels (Hajek *et al.*, 2014; Cai and Tyree, 2010; Hacke *et al.*,

2006). This was not the case in all genera studied since, in contrast with our results; vessel density and length, rather than vessel diameter (Lens *et al.*, 2010) played a role in embolism resistance in *Acer* species. Jacobsen *et al.* (2005) found that the effect of vessel density on embolism resistance is due to its role in modifying fiber properties in wood. A reverse pattern was observed in the genus *Cistus*, where species with narrow vessels were found to be more prone to xylem embolism in the Mediterranean region (Torres-Ruiz *et al.*, 2017b). Gleason *et al.* (2016) tested this trade-off across many angiosperms and gymnosperm species and found a positive correlation between hydraulic conductivity and P_{50} and concluded that there is a weak tradeoff between hydraulic efficiency and safety among species. Unlike the interspecific pattern, we found an opposite trend at the intraspecific level with no significant difference among *Q. petraea* provenances in P_{50} value. Regardless of the provenance, individual trees within a provenance having lower P_{50} tend to have larger vessel sizes. These contrasting trends between P_{50} and vessel diameter suggest that vulnerability to embolism not only depends on the size of the vessels but also on other traits. In fact, Li *et al.* (2016) reported recently that the thickness of the pit membranes between two adjoining vessels plays a major role in plant resistance to embolism. To explain the contrasting trends when comparing species or provenances within a given species, it would be necessary to evaluate if changes in pit membrane thickness are related to the diameter of the xylem vessels and how this possible relationship changes within and among species. Indeed, the link between vessel size and vulnerability to embolism might be indirect in angiosperms such as oak, and the ease of air-seeding could be driven by the single tiniest pit membrane of a vessel.

Conclusions

Our results in oaks confirm earlier data obtained in other genera (Lamy *et al.*, 2011, 2014) showing that vulnerability to embolism exhibits significant between-species and substantial within-population variation, but lacks between-population variation. Assuming that the within-population component of variation is partly due to genetic effects, our results suggest that there is potential for divergent evolution between populations. As no population differentiation is actually observed, we may conclude that either differentiation is so narrow that it could not be detected by existing technologies. We may also conclude that selection is constrained and canalized, or that selection is uniform across all populations. Another probable explanation could be that vulnerability to embolism is neutral. Each of these interpretations raises new avenues of research along technological and biological pathways. An immediate concern is to evaluate the adaptive value of the hydraulic parameters derived from the cavitron technique (P_{50}) under controlled conditions, or in nature by assessing their selection gradients.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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References

- Aitken SN, Bemmels JB. Time to get moving: assisted gene flow of forest trees. *Evolutionary Applications*. 2016; 9:271–290. [PubMed: 27087852]
- Allen CD, Macalady AK, Chenchouni H, et al. Cobb N. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*. 2010; 259:660–684.
- Anderegg WRL, Klein T, Bartlett M, Sack L, Pellegrini AFA, Choat B, Jansen S. Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences*. 2016; 113(18):5024–5029.
- Anderegg WRL. Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. *New Phytologist*. 2015; 205:1008–1014. [PubMed: 25729797]
- Anderegg WRL, Kane JM, Anderegg LDL. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*. 2013; 3:30–36.
- Arend M, Kuster T, Günthardt-Goerg MS, Dobbervin M. Provenance-specific growth responses to drought and air warming in three European oak species (*Quercus robur*, *Q. petraea* and *Q. pubescens*). *Tree Physiology*. 2011; 31:287–297. [PubMed: 21422189]
- Bacilieri R, Ducousso A, Petit RJ, Kremer A. Mating System and Asymmetric Hybridization in a Mixed Stand of European Oaks. *Evolution*. 1996; 50:900–908. [PubMed: 28568948]
- Baquetano FJ, Castillo FJ. Drought tolerance in the Mediterranean species *Quercus coccifera*, *Quercus ilex*, *Pinus halepensis*, and *Juniperus phoenicea*. *Photosynthetica*. 2007; 45:229–238.
- Barigah TS, Charrier O, Douris M, Bonhomme M, Herbette S, Améglio T, Fichot R, Brignolas F, Cochard H. Water stress-induced xylem hydraulic failure is a causal factor of tree mortality in beech and poplar. *Annals of Botany*. 2013; 112:1431–1437. [PubMed: 24081280]
- Bouche PS, Larter M, Domec JC, Burlett R, Gasson P, Jansen S, Delzon S. A broad survey of hydraulic and mechanical safety in the xylem of conifers. *Journal of Experimental Botany*. 2014; 65:4419–4431. [PubMed: 24916072]
- Brodribb TJ, Bowman DJMS, Nichols S, Delzon S, Burlett R. Xylem function and growth rate interact to determine recovery rates after exposure to extreme water deficit. *New Phytologist*. 2010; 188:533–542. [PubMed: 20673281]
- Brodribb TJ, Cochard H. Hydraulic Failure Defines the Recovery and Point of Death in Water-Stressed Conifers. *Plant Physiology*. 2009; 149:575–584. [PubMed: 19011001]
- Cailleret M, Jansen S, Robert EMR, et al. Martínez-Vilalta J. A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology*. 2017; 23:1675–1690. [PubMed: 27759919]
- Cai J, Tyree MT. The impact of vessel size in vulnerability curves: data and models for within-species variability in saplings of aspen, *Populus tremuloides* Michx. *Plant Cell & Environment*. 2010; 33:1059–1069.
- Choat B, Badel E, Burlett R, Delzon S, Cochard H, Jansen S. Non-invasive measurement of vulnerability to drought induced embolism by X-ray microtomography. *Plant Physiology*. 2015 15.00732.
- Choat B, Jansen S, Brodribb TJ, et al. Zanne AE. Global convergence in the vulnerability of forests to drought. *Nature*. 2012; 491:752–755. [PubMed: 23172141]
- Cochard H, Badel E, Herbette S, Delzon S, Choat B, Jansen S. Methods for measuring plant vulnerability to cavitation: a critical review. *Journal of Experimental Botany*. 2013; 64(15):4779–4791. [PubMed: 23888067]
- Cochard H, Herbette S, Barigah T, Badel E, Ennajeh M, Vilagrosa A. Does sample length influence the shape of xylem embolism vulnerability curves? A test with the Cavitron spinning technique. *Plant Cell & Environment*. 2010; 33:1543–1552.

- Cochard H, Damour G, Bodet C, Tharwat I, Poirier M, Améglio T. Evaluation of a new centrifuge technique for rapid generation of xylem vulnerability curves. *Physiol Plantarum*. 2005; 124:410–418.
- Cochard H. A technique for measuring xylem hydraulic conductance under high negative pressures. *Plant, Cell & Environment*. 2002; 25:815–819.
- Cochard H, Bréda N, Granier A, Aussenac G. Vulnerability to air embolism of three European oak species (*Quercus petraea* (Matt) Liebl, *Q pubescens* Willd, *Q robur* L). *Annales des sciences forestieres*. 1992; 49(3):225–233.
- Corcuera L, Cochard H, Gil-Pelegrin E, Notivol E. Phenotypic plasticity in mesic populations of *Pinus pinaster* improves resistance to xylem embolism (P_{50}) under severe drought. *Trees*. 2011; 25:1033.
- David TS, Henriques MO, Kurz-Besson C, et al. David JS. Water-use strategies in two co-occurring Mediterranean evergreen oaks: surviving the summer drought. *Tree Physiology*. 2007; 27:793–803. [PubMed: 17331898]
- David-Schwartz R, Paudel I, Mizrahi M, et al. Cohen S. Indirect evidence for genetic differentiation in vulnerability to embolism in *Pinus halepensis*. *Frontiers in Plant Science*. 2016; 7
- Delzon S. New insight into leaf drought tolerance. *Functional Ecology*. 2015; 29:1247–1249.
- Delzon S, Urli M, Samalens JC, Lamy JB, Lischke H, Sin F, Zimmermann NE, Porté AJ. Field Evidence of Colonisation by Holm Oak, at the Northern Margin of Its Distribution Range, during the Anthropocene Period. *PloS one*. 2013; 8:e80443. [PubMed: 24260391]
- Delzon S, Douthe C, Sala A, Cochard H. Mechanism of water-stress induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal capillary-seeding. *Plant, Cell & Environment*. 2010; 33:2101–2111.
- Ducousso, A., Bordacs, S. EUFORGEN Technical Guidelines for genetic conservation and use for Pedunculate and sessile oaks (*Quercus robur*) and (*Quercus petraea*). Bioversity International; 2004.
- Eaton, E., Caudullo, G., Oliveira, S., de Rigo, D. *Quercus robur* and *Quercus petraea* in Europe: distribution, habitat, usage and threats. European Atlas of Forest Tree Species. San-Miguel-Ayanz, J.de Rigo, D.Caudullo, G.Houston Durrant, T., Mauri, A., editors. Publication Office of the European Union; Luxembourg: 2016. p. 160-163.
- Ennajeh M, Simões F, Khemira H, Cochard H. How reliable is the double-ended pressure sleeve technique for assessing xylem vulnerability to cavitation in woody angiosperms? *Physiologia Plantarum*. 2011; 142:205–210. [PubMed: 21401617]
- Epron D, Dreyer E. Long-term effects of drought on photosynthesis of adult oak trees [*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.] in a natural stand. *New Phytologist*. 1993; 125:381–389.
- EUFORGEN. Distribution maps of Sessile oak (*Quercus petraea*), Pedunculate oak (*Quercus robur*) and Cork oak (*Quercus suber*). 2009. www.euforgen.org
- Gerber S, Chadœuf J, Gugerli F, et al. Kremer A. High Rates of Gene Flow by Pollen and Seed in Oak Populations across Europe. *PloS one*. 2014; 9:e85130. [PubMed: 24454802]
- Gimeno TE, Pías B, Lemos-Filho JP, Valladares F. Plasticity and stress tolerance override local adaptation in the responses of Mediterranean holm oak seedlings to drought and cold. *Tree Physiology*. 2009; 29:87–98. [PubMed: 19203935]
- Gleason SM, Westoby M, Jansen S, et al. Zanne AE. Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist*. 2016; 209:123–136. [PubMed: 26378984]
- Hacke UG, Sperry JS, Wheeler JK, Castro L. Scaling of angiosperm xylem structure with safety and efficiency. *Tree Physiology*. 2006; 26:689–701. [PubMed: 16510385]
- Hajek P, Kurjak D, von Wühlisch G, Delzon S, Schuldt B. Intraspecific Variation in Wood Anatomical, Hydraulic, and Foliar Traits in Ten European Beech Provenances Differing in Growth Yield. *Frontiers in Plant Science*. 2016; 7:791. [PubMed: 27379112]
- Hajek P, Leuschner C, Hertel D, Delzon S, Schuldt B. Trade-offs between xylem hydraulic properties, wood anatomy and yield in *Populus*. *Tree Physiology*. 2014; 34:744–756. [PubMed: 25009155]
- Hoffmann WA, Marchin RM, Abit P, Lau OL. Hydraulic failure and tree dieback are associated with high wood density in a temperate forest under extreme drought. *Global Change Biology*. 2011; 17:2731–2742.

- Hubert F, Grimm GW, Joussein E, Berry V, Franc A, Kremer A. Multiple nuclear genes stabilize the phylogenetic backbone of the genus *Quercus*. *Systematics and Biodiversity*. 2014; 12:405–423.
- Jacobsen AL, Pratt RB, Ewers FW, Davis SD. Cavitation resistance among twenty-six chaparral species of southern California. *Ecological Monographs*. 2007; 77:99–115.
- Jacobsen AL, Ewers FW, Pratt RB, Paddock WA, Davis SD. Do Xylem Fibers Affect Vessel Cavitation Resistance? *Plant Physiology*. 2005; 139:546–556. [PubMed: 16100359]
- Kremer A, Potts BM, Delzon S. Genetic divergence in forest trees: understanding the consequences of climate change. *Functional Ecology*. 2014; 28:22–36.
- Kremer A, Ronce O, Robledo-Arnuncio JJ, et al. Schueler S. Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecology Letters*. 2012; 15:378–392. [PubMed: 22372546]
- Lamy JB, Delzon S, Bouche PS, Alia R, Vendramin GG, Cochard H, Plomion C. Limited genetic variability and phenotypic plasticity detected for cavitation resistance in a Mediterranean pine. *New Phytologist*. 2014; 201:874–886. [PubMed: 24180459]
- Lamy JB, Bouffier L, Burlett R, Plomion C, Cochard H, Delzon S. Uniform Selection as a Primary Force Reducing Population Genetic Differentiation of Cavitation Resistance across a Species Range. *PloS one*. 2011; 6:e23476. [PubMed: 21858137]
- Lens F, Sperry JS, Christman MA, Choat B, Rabaey D, Jansen S. Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus *Acer*. *New Phytologist*. 2010; 190:709–723. [PubMed: 21054413]
- Li S, Lens F, Espino S, Karimi Z, Klepsch M, Schenk HJ, Schmitt M, Schuldt B, Jansen S. Intervessel pit membrane thickness as a key determinant of embolism resistance in angiosperm xylem. *IAWA*. 2016; 37:152–171.
- Linton MJ, Sperry JS, Williams DG. Limits to water transport in *Juniperus osteosperma* and *Pinus edulis*: implications for drought tolerance and regulation of transpiration. *Functional Ecology*. 1998; 12:906–911.
- Little, EL. Atlas of United States trees, volume 1, conifers and important hardwoods. U.S. Department of Agriculture Miscellaneous Publication 1146; 1971. p. 9
- Lloret F, Siscart D, Dalmases C. Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). *Global Change Biology*. 2004; 10:2092–2099.
- Lowe AJ, Cavers S, Boshier D, Breed MF, Hollingsworth PM. The resilience of forest fragmentation genetics-no longer a paradox-we were just looking in the wrong place. *Heredity*. 2015; 115:97–99. [PubMed: 26176685]
- Maherali H, Pockman WT, Jackson RB. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology*. 2004; 85:2184–2199.
- Martin-StPaul NK, Longepierre D, Huc R, Delzon S, Burlett R, Joffre R, Rambal S, Cochard H. How reliable are methods to assess xylem vulnerability to cavitation? The issue of ‘open vessel’ artifact in oaks. *Tree Physiology*. 2014; 34(8):894–905. [PubMed: 25074860]
- McCarthy JJ, Dawson JO. Growth and water use efficiency of *Quercus alba*, *Q. bicolor*, *Q. imbricaria* and *Q. palustris* seedlings under conditions of reduced soil water availability and solar irradiance. *Transactions of the Illinois State Academy of Science*. 1990; 83:128–148.
- McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, Yezzer EA. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*. 2008; 178:719–739. [PubMed: 18422905]
- McElrone AJ, Brodersen CR, Alsina MM, et al. Choat B. Centrifuge technique consistently overestimates vulnerability to water stress-induced cavitation in grapevines as confirmed with high-resolution computed tomography. *New Phytologist*. 2012; 196:661–665. [PubMed: 22803744]
- Meinzer FC, Johnson DM, Lachenbruch B, McCulloh KA, Woodruff DR. Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology*. 2009; 23:922–930.
- Bréda N, Huc R, Granier A, Dreyer E. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*. 2006; 63:625–644.

- Oh SH, Manos PS. Molecular phylogenetics and cupule evolution in Fagaceae as inferred from nuclear CRABS CLAW sequences. *Taxon*. 2008; 57:434–451.
- Pammenter NV, Vander Willigen C. A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiology*. 1998; 18:589–593. [PubMed: 12651346]
- Petit RJ, Csaikl UM, Bordács S, et al. Finkeldey R. Chloroplast DNA variation in European white oaks: phylogeography and patterns of diversity based on data from over 2600 populations. *Forest Ecology and Management*. 2002; 156(1):5–26.
- Pivovarov AL, Burlett R, Lavigne B, Cochard H, Santiago LS, Delzon S. Testing the ‘microbubble effect’ using the Cavitron technique to measure xylem water extraction curves. *AoB Plants*. 2016; 8 lw011.
- Reyer C, Lasch-Born P, Suckow F, Gutsch M, Murawski A, Pilz T. Projections of regional changes in forest net primary productivity for different tree species in Europe driven by climate change and carbon dioxide. *Annals of forest science*. 2014; 71:211–225.
- Sade N, Alem G, Moshelion M. Risk-taking plants. Anisohydric behavior as a stress-resistance trait. *Plant Signal Behaviour*. 2012; 7:1–4.
- Sanders TGM, Pitman R, Broadmeadow MSJ. Species-specific climate response of oaks (*Quercus spp.*) under identical environmental conditions. *iForest*. 2013; 7:61–69.
- Scotti I, González-Martínez SC, Budde KB, Lalagüe H. Fifty years of genetic studies: what to make of the large amounts of variation found within populations? *Annals of forest science*. 2016; 73:69–75.
- Sáenz-Romero C, Lamy JB, Loya-Rebollar E, et al. Delzon S. Genetic variation of drought-induced cavitation resistance among *Pinus hartwegii* populations from an altitudinal gradient. *Acta Physiologiae Plantarum*. 2013; 35:2905.
- Sperry JS, Nichols KL, Sullivan JEM, Eastlack SE. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of Northern Utah and Interior Alaska. *Ecology*. 1994; 75:1736–1752.
- Talhelm AF, Pregitzer KS, Kubiske ME, et al. Karnosky DF. Elevated carbon dioxide and ozone alter productivity and ecosystem carbon content in northern temperate forests. *Global Change Biology*. 2014; 20:2492–2504. [PubMed: 24604779]
- Thomsen JE, Bohrer G, Matheny AM, Ivanov VY, He L, Renninger HJ, Schäfer KV. Contrasting hydraulic strategies during dry soil conditions in *Quercus rubra* and *Acer rubrum* in a sandy site in Michigan. *Forests*. 2013; 4:1106–1120.
- Torres-Ruiz JM, Cochard H, Choat B, et al. Delzon S. Xylem resistance to embolism: presenting a simple diagnostic test for the open vessel artefact. *New Phytologist*. 2017a; doi: 10.1111/nph.14589
- Torres-Ruiz JM, Cochard H, Fonseca E, Badel E, Gazarini L, Vaz M. Differences in functional and xylem anatomical features allow *Cistus* species to co-occur and cope differently with drought in the Mediterranean region. *Tree Physiology*. 2017b; In press. doi: 10.1093/treephys/tpx013
- Torres-Ruiz JM, Jansen S, Choat B, McElrone AJ, Cochard H, Brodribb TJ, Badel E, Burlett R, Bouche PS, Brodersen CR. Direct X-ray microtomography observation confirms the induction of embolism upon xylem cutting under tension. *Plant Physiology*. 2015; 167:40–43. [PubMed: 25378693]
- Torres-Ruiz JM, Cochard H, Mayr S, Beikircher B, Diaz-Espejo A, Rodriguez-Dominguez CM, Badel E, Fernández JE. Vulnerability to cavitation in *Olea europaea* current-year shoots: further evidence of an open-vessel artifact associated with centrifuge and air-injection techniques. *Physiologia Plantarum*. 2014; 152:465–474. [PubMed: 24611594]
- Trueba S, Pouteau R, Lens F, Feild TS, Isnard S, Olson ME, Delzon S. Vulnerability to xylem embolism as a major correlate of the environmental distribution of rainforest species on a tropical island. *Plant Cell & Environment*. 2017; 40:277–289.
- Tyree MT, Zimmermann MH. Hydraulic Architecture of Whole Plants and Plant Performance. Xylem Structure and the Ascent of Sap. Tyree, MT., Zimmermann, MH., editors. Springer Berlin Heidelberg; Berlin, Heidelberg: 2002. p. 175–214.
- Urli M, Lamy JB, Sin F, Burlett R, Delzon S, Porté AJ. The high vulnerability of *Quercus robur* to drought at its southern margin paves the way for *Quercus ilex*. *Plant Ecology*. 2014; 216:177–187.

- Urli M, Porté AJ, Cochard H, Guengant Y, Burlett R, Delzon S. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiology*. 2013; 33:672–683. [PubMed: 23658197]
- Venturas MD, Sperry JS, Hacke UG. Plant xylem hydraulics: What we understand, current research, and future challenges. *Journal of Integrative Plant Biology*. 2017; 59:356–389. [PubMed: 28296168]
- Venturas MD, Rodriguez-Zaccaro FD, Percolla MI, Crous CJ, Jacobsen AL, Pratt RB. Single vessel air injection estimates of xylem resistance to cavitation are affected by vessel network characteristics and sample length. *Tree Physiology*. 2016; 36:1247–1259. [PubMed: 27358206]
- Wheeler JK, Huggett BA, Tofte AN, Rockwell FE, Holbrook NM. Cutting xylem under tension or supersaturated with gas can generate PLC and the appearance of rapid recovery from embolism. *Plant Cell & Environment*. 2013; 36:1938–1949.
- Wortemann R, Herbette S, Barigah T, Fumanal B, Alia R, Ducousso A, Gomory D, Roeckel-Drevet P, Cochard H. Genotypic variability and phenotypic plasticity of cavitation resistance in *Fagus sylvatica* L. across Europe. *Tree Physiology*. 2011; 31:1175–1182. [PubMed: 21989814]

Fig. 1.
Q. petraea provenances (full circles) planted in the common garden experiment located in the core of the species distribution range (full star) (Map source: EUFORGEN)

Fig. 2.

Vulnerability curves obtained with the in situ flow centrifuge (Cavitron). They were constructed using the 1 meter diameter rotor in the Cavitron. Each color corresponds to a different individual within each species

Fig. 3.

Mean vulnerability curves for each of the 6 studied oak species showing percentage loss of hydraulic conductance in xylem (%) as a function of xylem pressure (MPa). Shaded bands represent standard errors, and 50% loss in conductance is indicated by a horizontal dotted line

Fig. 4.

Mean vulnerability curves for each of the 4 studied sessile oak provenances showing percentage loss of hydraulic conductance in xylem (%) as a function of xylem pressure (MPa). Shaded bands represent standard errors, and 50% loss in conductance is indicated by a horizontal dotted line

Fig. 5. Weighted regression between P_{50} and d_h (hydraulically weighted vessel diameter in μm) among the 6 oak species (left) and among the four provenances within *Q. petraea* (right), mean values per species/provenance is indicated by stars, d_h = hydraulically weighted vessel diameter (μm); P_{50} = water potential at 50% loss of conductivity (MPa)

Table 1Climatic data, location and elevation of the studied *Q. petraea* provenances

Provenance	Country	Latitude	Longitude	Altitude (m)	MAT	MAP	MAE	AI
Grésigne	France	44.04	1.75	310	11.9	806	995	0.81
Killarney	Ireland	52.01	-9.50	50	10.1	1374	657	2.09
Vachères	France	43.98	5.63	650	10.7	779	847	0.92
Göhrde	Germany	53.10	10.85	85	8.4	629	699	0.90

MAT = mean annual temperature (°C), MAP = Mean Annual Precipitation (mm), MAE = Mean Annual Potential Evapotranspiration, AI = aridity index

Table 2

Xylem embolism vulnerability parameters of the six studied oak species. Different letters indicate significant differences between species, (p-value in parenthesis)

Species	n	P_{50}	P_{12}	P_{88}	S	CV
<i>Quercus ilex</i>	10	-7.13 (0.16) c	-4.93 (0.29) c	-9.33 (0.23) d	24.98(2.24) a	7.27
<i>Quercus palustris</i>	5	-5.74 (0.18) b	-3.53 (0.47) b	-7.95 (0.33) c	26.87(6.41) a	6.97
<i>Quercus petraea</i>	16	-4.61 (0.11) a	-3.55 (0.19) b	-5.67 (0.17) a	79.54(23.31) a	9.78
<i>Quercus robur</i>	8	-4.74 (0.09) a	-3.81 (0.20) b	-5.66 (0.09) a	67.07(14.09) a	5.17
<i>Quercus rubra</i>	6	-4.43 (0.25) a	-2.14 (0.48) a	-6.72 (0.29) b	24.52(4.08) a	13.72
<i>Quercus suber</i>	7	-5.52 (0.28) b	-3.12 (0.42) b	-7.93 (0.44) c	24.00(4.07) a	13.25

n = number of samples; P_{50} , P_{12} and P_{88} are water potential values at 50%, 12% and 88% loss of conductivity respectively; S = slope of vulnerability curve; CV = coefficient of variation in P_{50} (%)

Table 3

Xylem embolism vulnerability parameters of the four sessile oak provenances. Different letters indicate significant differences between species, (p-value in parenthesis)

Species	n	P_{50}	P_{12}	P_{88}	S	CV_{intra}
Grésigne	12	-4.58(0.14) _a	-3.42(0.19) _a	-5.74(0.20) _a	53.05(7.96) _a	10.28
Killarney	13	-4.65(0.19) _a	-3.72(0.14) _a	-5.59(0.31) _a	77.70(15.91) _a	14.78
Vachères	14	-4.64(0.10) _a	-3.51(0.20) _a	-5.78(0.14) _a	52.95(5.80) _a	8.15
Göhrde	15	-4.31(0.10) _a	-3.10(0.20) _a	-5.52(0.14) _a	49.44(5.18) _a	9.00

n = number of samples; P_{50} , P_{12} and P_{88} are water potential at 50%, 12% and 88% loss of conductivity respectively; S = slope of vulnerability curve; CV_{intra} = coefficient of variation in P_{50} within provenance (%)

Table 4Pearson correlation coefficient (r) between P_{50} and various anatomical traits

Trait	Anatomical traits	r	P- value
<i>Among the 6 oak species</i>			
P_{50}	VD_{ring}	0.03	0.88
	VD	0.17	0.33
	d_{ring}	0.47	0.004
	d	0.31	0.07
	d_{h_ring}	0.63	<0.0001
	d_h	0.42	0.01
	K_{s_ring}	0.42	0.01
	K_s	0.28	0.09
<i>Within Q. petraea</i>			
P_{50}	VD_{ring}	-0.05	0.78
	VD	-0.01	0.95
	d_{ring}	-0.30	0.06
	d	-0.41	0.01
	d_{h_ring}	-0.35	0.03
	d_h	-0.45	0.004
	K_{s_ring}	-0.29	0.08
	K_s	-0.46	0.004

VD_{ring} = vessel density of the last ring (n mm^{-2}), VD = vessel density (n mm^{-2}), d_{ring} = vessel diameter of the last ring (μm), d = vessel diameter (μm), d_h = hydraulically weighted vessel diameter (μm), d_{h_ring} = hydraulically weighted vessel diameter of the last ring (μm), K_s = relative theoretical conductivity ($\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$), K_{s_ring} = relative theoretical conductivity of the last ring ($\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$), P_{50} = water potential at 50% loss of conductivity (MPa).