Forest Ecology and Management 424 (2018) 53–61

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

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ARTICLE INFO

Keywords:
Plant hydraulics
Xylem embolism
Drought resistance
Climate change
Oaks

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. However, the presence of long vessels makes it difficult to assess xylem vulnerability to embolism in these species. Thanks to the development of a 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 between 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 between 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 and a higher amount of hydraulic bridges between vessels. However, this tradeoff between hydraulic efficiency and safety was not observed between *Q. petraea* provenances.

1. 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 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 more likely due to xylem hydraulic failure (Anderegg et al., 2013, 2016) caused by the formation of air bubbles (embolism) in the xylem conduits rather than carbon starvation (Adams et al., 2017) even if we cannot totally exclude this hypothesis (Hartmann 2015). Xylem embolism disrupts the water transport from the roots to the leaves (Tyree & Zimmermann, 2002) and lead to organ desiccation and plant death (Urli et al. 2013). 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 and Cochard, 2009; Brodribb et al., 2010; Barigah et al., 2013; Meinzer et al., 2009; Torres-Ruiz et al., 2017a; Urli et al., 2013).

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https://doi.org/10.1016/j.foreco.2018.04.031
Received 28 November 2017; Received in revised form 20 February 2018; Accepted 17 April 2018

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).

Between-species variation in resistance to embolism was earlier reported in conifers (Bouche et al., 2014; Delzon et al., 2010) and angiospermas (Torres-Ruiz et al., 2017b). It is also reported that within-species variation can be considerably less than the between-species variation (David-Schwartz et al., 2016; Lamy et al., 2014). Intraspecific variability in resistance to embolism in conifers can be of lower magnitude than intraspecific variability in angiosperms (Anderegg, 2015) although such studies are very limited in number. At the intraspecific level, variation in resistance to embolism is largely attributed to environmental factors rather than genetics as observed in several species such as *Fagus sylvatica* (Schuldt et al., 2016; Aranda et al., 2015) and *Pinus pinaster* (Lamy et al. 2014). 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 70 cm has been typically reported (Cochard and Tyree 1990; Jacobsen et al. 2007). The vulnerability to embolism may had been overestimated in previous studies due to both the so called "open-vessel" (Cochard et al. 2013; Torres-Ruiz et al. 2014, 2017a) and "cutting" (Wheeler et al., 2013; Torres-Ruiz et al., 2015) artefacts. The overestimations are especially evident by using centrifuge techniques as the 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 et al., 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 and 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. Although there are many studies within the genus *Quercus* reporting difference in functional traits between oak species under drought (Chiatante et al. 2015; Peguero-Pina et al. 2014), an accurate quantification of the interspecific variation in resistance to embolism within the genus is still lacking. This scientific gap is mainly due to the difficulty in measuring long vesselled species while avoiding the open vessel artefact described above. In a recent review, Robert et al. (2017) reported that the average P_{50} value of oaks highly differ whether all vulnerability curves or s-shaped curves only are considered. This result confirms the urgent need to better characterize hydraulic traits in oaks. Moreover, experimental evidence of the adaptive significance of the resistance to embolism is also absent in oaks. Therefore, an evaluation of the 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 variation in xylem vulnerability to embolism between six oak species (*Quercus* spp.) widely distributed in Europe. Vulnerability to embolism was assessed by using a newly developed prototype of Cavitron equipped with a 1 m-diameter rotor (Charrier et al. 2018). 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.

2. Materials and methods

2.1. Interspecific variation in xylem vulnerability to embolism for six 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 the same climatic conditions in Southern France (INRA and University of Bordeaux campus). All branches were 3–5 years old and were a minimum of two meters long ranging between 18 and 20 mm in diameter. They were 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).

2.2. Intraspecific variation in xylem vulnerability to embolism for Quercus petraea

For evaluating the genetic differentiation in vulnerability to embolism between *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 12–15 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 2 m long branches were cut from upper part of the tree. Branches were wrapped in wet paper before being immediately transported to the lab