Forest Ecology and Management 285 (2012) 1–10

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

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

Drought-induced embolism in current-year shoots of two Mediterranean evergreen oaks

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ARTICLE INFO

Article history:
Received 14 April 2012
Received in revised form 3 August 2012
Accepted 4 August 2012
Available online 1 September 2012

Keywords:
Quercus suber
Quercus ilex
Vulnerability curves
Hydraulic conductivity
Xylem anatomy
Hydraulic safety margins

ABSTRACT

Quercus suber and *Quercus ilex* trees are major elements of Mediterranean landscapes, which are threatened by the increasing water deficits related to climate change. To contribute to the understanding of the capacity of these oaks to withstand severe drought we assessed the vulnerability to xylem embolism and the anatomical traits in current-year shoots. Data were collected in mature trees at two sites, in central/coastal and southern/inland Portugal. *In situ* safety margins to hydraulic failure were evaluated from long-term predawn and midday leaf water potential records. Results showed that xylem vulnerability to embolism was similar in *Q. ilex* and *Q. suber*. The 50% loss in hydraulic conductivity ($\Psi_{xyl,50PLC}$) was observed at xylem water potentials of −2.9 and −3.2 MPa in shoots of *Q. suber* and *Q. ilex*, respectively. Values of mean vessel diameter of *Q. suber* shoots at both sites suggest an intra-species adaptation to the local water availability, with larger vessels at the more mesic site. *In situ* hydraulic safety margins observed in shoots showed that, even during the driest periods, both oaks lived comfortably above the most critical embolism thresholds. However, the hydraulic safety margins were narrower in the driest site. Results are relevant to the understanding of survival, growth, and functional behaviour of evergreen oaks in Mediterranean climates, under recurrent/seasonal drought conditions.

1. Introduction

In recent decades there were many reports of enhanced tree mortality rates in forests of all ages, especially in temperate regions (van Mantgem et al., 2009), but also in Mediterranean-type climates (Lloret et al., 2004). Plausible causes are increasing water deficits related to global warming (van Mantgem et al., 2009), which may result in the failure of the hydraulic system of trees (Ryan, 2011), associated or not to starvation and depletion of carbon reserves (McDowell et al., 2011). During dry periods water stress may induce xylem cavitation and the formation of embolisms, resulting in the disruption of water columns and in the reduction of water supply to leaves (Tyree and Zimmermann, 2002). Xylem embolism caused by severe drought stress has been considered one of the major factors affecting plant productivity and survival (Tyree and Sperry, 1988). Mediterranean-climate regions are characterised by recurrent droughts, with irregular/limited rainfall and high evaporative demand. Climate change scenarios for the Western Mediterranean Basin foresee warmer air temperatures and an increase in the length and intensity of the seasonal summer drought (Miranda et al., 2002). Trees cope with these seasonal water shortages by preventing water losses through stomatal closure and maximising the soil and groundwater uptake by deep roots (Canadell et al., 1996; David et al., 2007; Maherali et al., 2004). Under extreme drought, stomatal regulation may not be enough to maintain leaf water potential above a critical threshold and catastrophic embolism may occur (Sperry, 1986).

Mediterranean evergreen oak woodlands (*montados* in Portugal and *dehesas* in Spain) characterise the landscape of extensive areas of the Iberian Peninsula and are ecosystems of a high socioeconomic and conservation value (Bugalho et al., 2011). In Central-Southern Portugal, *Quercus suber* L. (cork oak) and *Quercus ilex* spp. *rotundifolia* Lam. syn. *ballota* (holm oak) are the dominant

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http://dx.doi.org/10.1016/j.foreco.2012.08.005

species. Although co-occurring in some places, *Q. ilex* prevails in the inner, drier regions and *Q. suber* in the wetter, coastal and montane areas. This geographic distribution, though influenced by human activity, seems to mainly reflect the lesser drought resistance of *Q. suber* (David et al., 2007). Extensive literature is available concerning the xylem vulnerability to embolism and other hydraulic traits of *Q. ilex* (Corcuera et al., 2004; Gartner et al., 2003; Limousin et al., 2010; Lo Gullo and Salleo, 1993; Martínez-Vilalta et al., 2002; Tognetti et al., 1998; Villar-Salvador et al., 1997) and of other Mediterranean species (Iovi et al., 2009). However, *Q. suber* has been much less studied (Lo Gullo et al., 2003; Tyree and Cochard, 1996; Vaz et al., 2012). To our knowledge, its vulnerability to drought-induced embolism has not yet been fully characterised particularly in adult trees.

We aimed to evaluate and compare the xylem conducting efficiency and vulnerability of current-year shoots of *Q. suber* and *Q. ilex* to drought induced cavitation. Measurements and sampling were done in mature trees at two different sites, located in Central (Lezirias) and Southern (Mitra) Portugal. Cork oak was studied at Lezirias and Mitra whereas holm oak was only studied at Mitra. We hypothesised that: (1) *Q. ilex* xylem would be less prone to hydraulic failure than *Q. suber*, and the difference would be enough to explain the geographic distribution of the two species; (2) Differences in site water availability might reflect in small intra-species variations in the vulnerability to embolism and xylem anatomy. The specific objectives of this work were to: (1) measure xylem vulnerability to embolism in current-year shoots of mature cork and holm oak trees; (2) test intra-species differences in vulnerability to embolism and xylem anatomy of cork oak shoots between sites; (3) evaluate if species are living close to their hydraulic limits, by estimating the *in situ* minimum safety margins.

2. Material and methods

2.1. Study sites and plant material

The study was carried out at two evergreen oak woodlands 90 km apart, in Central (Lezirias site) and Southern (Mitra site) Portugal. The Mitra site (38°32′N, 8°00′W) has an inland location near the town of Évora, at the ‘‘Herdade da Alfarrobeira’’ (ca. 150 km South-East of Lisbon), in a sparse mixed stand where *Q. ilex* dominates and *Q. suber* occurs in scattered patches. At this site two single species plots (150 m apart) were established. The soil is a 1 m deep Dystric Cambisol (FAO, 1988), with low water retention capacity, overlying a granite bedrock. The Lezirias site (38°50′N, 8°49′W) is located near the coast, at the estate of ‘‘Companhia das Lezirias’’, about 50 km East of Lisbon, in a pure *Q. suber* stand. The soil is a deep Arenosol (FAO, 1988), with high permeability and low water retention capacity, overlying a thick clay layer at ca. 9 m depth. The climate is Mediterranean at both sites, with hot dry summers and wet mild winters. Rainfall occurs predominantly from October to April. Long-term (1951–1980) mean annual rainfall and open water evaporation are 665 and 1760 mm for Mitra (the more xeric site), and 708 and 1347 mm for Lezirias, respectively (INMG, 1991a, 1991b). Mean annual temperature is 15.0 °C at Mitra, ranging from 8.6 °C in January to 23.1 °C in August, and 15.6 °C at Lezirias, ranging from 9.9 °C in January to 22.0 °C in August (INMG, 1991a, 1991b).

Hydraulic and anatomy measurements were done in 2007–2008 on four mature trees per species and site. Mean morphometric data of the sampled trees are given in Table 1. Tree age is about 60 years at Lezirias and 70 (*Q. ilex*) – 80 (*Q. suber*) years at Mitra. Average annual growth of current-year shoots was 5 cm and 3–4 cm for *Q. ilex* and *Q. suber* at Mitra, respectively, and 7–20 cm for *Q. suber* at Lezirias (Pinto et al., 2011). Branches of *Q. suber* were sampled from both sites, whereas branches of *Q. ilex* trees were only sampled from the Mitra site. *In situ* leaf and xylem water potential measurements were done in the same trees used for branch sampling.

Table 1
Mean (standard deviation, SD) morphometric data of the four sampled trees (*Q. suber* and *Q. ilex*) at the experimental sites.

Site	Species	DBH (m)	Height (m)	Crown projected area (m^2)
Lezirias	*Q. suber*	0.73 (0.18)	12.82 (1.16)	208.1 (32.4)
Mitra	*Q. suber*	0.49 (0.04)	9.05 (0.44)	128.7 (25.8)
Mitra	*Q. ilex*	0.40 (0.05)	7.63 (0.48)	60.2 (20.2)

DBH is diameter at breast height.

2.2. Environmental variables

Solar radiation (CM6B, Kipp and Zonen, Delft, The Netherlands) and rainfall (tipping-bucket rain gauge recorder ARG100, Environmental Measurements, Gateshead, UK) were measured at both sites (2001–2003 at Mitra and 2006–2008 at Lezirias). Water table depth was also measured at both sites by pressure transducers (PDCR 830, Campbell Scientific) installed in boreholes. Data were recorded every 10 s and stored as 10 or 30 min averages or totals by CR10X data loggers (Campbell Scientific, Shepshed, UK).

2.3. ‘‘In situ’’ leaf water potentials

Leaf water potential (Ψ_l, MPa) was measured monthly at Mitra (2001–2003 for both plots) and Lezirias (2006–2008). Measurements were done in four mature trees per plot at predawn ($\Psi_{l,pd}$) and around midday ($\Psi_{l,md}$), using a Scholander pressure chamber (PMS 1000, PMS Instruments, Corvalis, Oregon, USA) (Scholander et al., 1965). At each sampling time, three to four leaves per tree were collected at similar heights from the South-facing part of the crowns, bagged, and immediately measured.

2.4. Vulnerability to xylem embolism

The degree of vulnerability to embolism was inferred from vulnerability curves (VCs), plotting the xylem water potential (Ψ_{xyl}, MPa) versus the corresponding percentage loss of hydraulic conductivity (*PLC*, %). We used the dehydration technique (Sperry, 1986; Sperry et al., 1988), considered as the most reliable (reference technique) (Choat et al., 2010; Cochard et al., 2005; Sperry et al., 2012).

The hydraulic conductivity (K_h, kg s^{-1} MPa^{-1} m) of shoot segments of both species was measured following Sperry et al. (1988), with a high precision flow meter, XYL'EM (Embolism Meter, Bronkhorst, Montigny-Les-Cormeilles, France). K_h was measured at low pressure ($2–3 \times 10^{-3}$ MPa), to minimise the displacement of air bubbles in open vessels. All segments were perfused with ultra-pure, deionized, degassed and filtered (0.2 μm) water with 10 mM KCl. K_h was calculated as the ratio between the flow through each segment and the corresponding hydrostatic pressure gradient. It was converted to specific hydraulic conductivity (K_s, kg s^{-1} MPa^{-1} m^{-1}) by dividing by the xylem cross-sectional area (m^2).

Prior to branch collection, the maximum length of xylem vessels was determined using the air infiltration method in the entire length of large branches (Zimmermann and Jeje, 1981). The longest vessels in *Q. suber* and *Q. ilex* stems were found to be 2.6 and 2.0 m, respectively. Hence, to avoid contamination by air entry upon cutting, only branches longer than 3 m were sampled, overnight, from the top third of the South-facing side of the crowns. At each sampling date, one or two large branches per tree (depending on crown