

The high vulnerability of *Quercus robur* to drought at its southern margin paves the way for *Quercus ilex*

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Abstract Populations growing at the warm margins of the species' range are more prone to experience higher water stress compared to populations inhabiting the core of their distribution. Thus, assessing tree vulnerability to drought is crucial to improve prediction of forest mortality and species range limits. We quantified the abundance of two oak species (*Quercus robur* and *Quercus ilex*) along a water stress gradient in a coastal forest located at the southern edge of the distribution of *Q. robur*. We assessed their ecophysiological responses to drought during a wet and a dry

year and determined their vulnerability to drought under field conditions. The abundance of *Q. ilex* was high all along the water stress gradient, whereas the abundance of *Q. robur* dramatically declined with decreasing water availability. During dry years, the level of native embolism was significantly higher for *Q. robur* than for *Q. ilex* due to species differences in vulnerability to xylem cavitation. *Q. robur* had a narrower hydraulic safety margin than *Q. ilex* and operated very close to the species threshold of hydraulic failure, making it highly vulnerable to drought-induced mortality. In the current context of increasing drought frequency and severity, survival of *Q. robur* populations will be threatened at warm range margins.

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Introduction

In the current context of rapid global changes, distribution ranges of many tree species are expected to shift toward higher latitudes or altitudes (Iverson and Prasad 2001; Bakkenes et al. 2002; Malcolm et al. 2002; Iverson et al. 2008; Morin et al. 2008; Nakao et al. 2011). These range shifts are the results of colonization and extirpation events of populations located at the colder and warmer limits of the species distribution

range, respectively. An increasing body of empirical studies has shown that tree species populations located at their colder limits moved poleward or upward due to global changes (e.g., Walther et al. 2005; Penuelas et al. 2007; Batllori and Gutierrez 2008; Beckage et al. 2008; Devi et al. 2008; Parolo and Rossi 2008; Zhu et al. 2012; Delzon et al. 2013). On the contrary, evidences of extirpation events at their warmer edges remain rare (Allen and Breshears 1998; Penuelas and Boada 2003; Beckage et al. 2008; Zhu et al. 2012; Urli et al. 2014). The difference in detecting colonization and extirpation events of populations located at each edge are explained by the apparent higher stability of local populations at their warmer limit compared to those located at the colder edge. Indeed, at the colder limit, warmer temperatures promote recruitment and then colonization events (new occurrence of individuals where they were absent); on the opposite, at the warmer edge, tree mortality can take several years and though adequate conditions for seedlings germination and establishment may decrease, recruitment may still occur (Jump et al. 2009).

However, the risk of extirpation events for populations located at the species warmer limits remains non-negligible, more particularly in the current context of increasing drought. It is crucial to understand and predict the risk of tree mortality induced by drought of populations located at their warmer limits. Indeed, the frequency of extreme climatic events such as severe droughts is expected to increase in the near future (Meehl and Tebaldi 2004; Burke et al. 2006; Jentsch et al. 2007). Such catastrophic droughts could alter tree growth (Waring 1987; Ciais et al. 2005; Bigler et al. 2006; Hogg et al. 2008; Michaelian et al. 2011; Eilmann and Rigling 2012; Sanchez-Salguero et al. 2012), tree survival (Pockman and Sperry 2000; Breshears et al. 2005; Bigler et al. 2006; Gitlin et al. 2006; van Mantgem and Stephenson 2007; Hogg et al. 2008; Galiano et al. 2010; Michaelian et al. 2011), and thus species distribution (Engelbrecht et al. 2007) as attested by recent global forest diebacks (Mueller et al. 2005; Allen et al. 2010). For instance, Allen and Breshears (1998) reported the occurrence of a rapid shift of ecotones, from a semiarid ponderosa pine forest to a pinyon-juniper woodland. This shift was probably driven by differences in sensitivity and survival to extreme drought between both species (Mueller et al. 2005; Hoffmann et al. 2011). Drought is a major abiotic factor altering the survival of tree species at the warmer

limits of their distribution ranges (Castro et al. 2004; Hampe and Petit 2005; Jump and Penuelas 2005; Morin et al. 2007). Consequently, to understand and predict shifts in tree species, it is necessary to assess their risk of mortality in response to drought by studying populations located at the warmer limits of their distributions.

The main cause of plant mortality in response to drought is hydraulic failure: the increase of embolized xylem conduits (formation of air or water vapor bubble inside a xylem conduit) reduces the plant's ability to transport water from roots to leaves (Tyree and Sperry 1989). Recent studies (Brodribb and Cochard 2009; Brodribb et al. 2010) demonstrated that 50 % of stem embolism led to death in conifer species, whereas death in angiosperm species occurred when plants experienced more than 88 % of stem embolism (Barigah et al. 2013, Urli et al. 2013). Trees can experience different levels of native embolism in the field in response to extreme drought as the consequence of differences in their xylem vulnerability. As embolism repair is not a daily event and rarely occurs in trees, the comparison of hydraulic safety margins between species can allow us to assess their risk of mortality under drought (Delzon and Cochard 2014). Commonly, hydraulic safety margins are calculated as the difference between the minimum water potential experienced in the field and the water potential inducing 12, 50, or 88 % of embolism (Meinzer et al. 2009). Choat et al. (2012) showed that 70 % of 226 forest species from 81 sites worldwide operated under narrow hydraulic safety margins and thus are highly threatened by extreme drought.

The aim of the current study was to examine the mortality risk induced by drought on pedunculate oak (*Quercus robur* L.) and holm oak (*Quercus ilex* L.) in a coastal forest of South-West France (Fig. 1a). Maritime pine (*Pinus pinaster*), and sclerophyllous and deciduous oaks, including *Q. robur* and *Q. ilex*, are the dominant trees of these coastal dune forests. *P. pinaster* was massively planted from the 19th century to date (Buffault 1942), but *Q. robur* and *Q. ilex* are still naturally present on the dunes where *Q. robur* is considered as a high patrimonial value species. *Q. ilex*, long considered as an undesirable species by the forest managers (Delzon et al. 2013), is now appreciated for its potential ecological (biodiversity) and forestry services. These populations of *Q. robur* and *Q. ilex* are located at the warmer edge and colder edge of their distribution range, respectively. Niche-based, growth

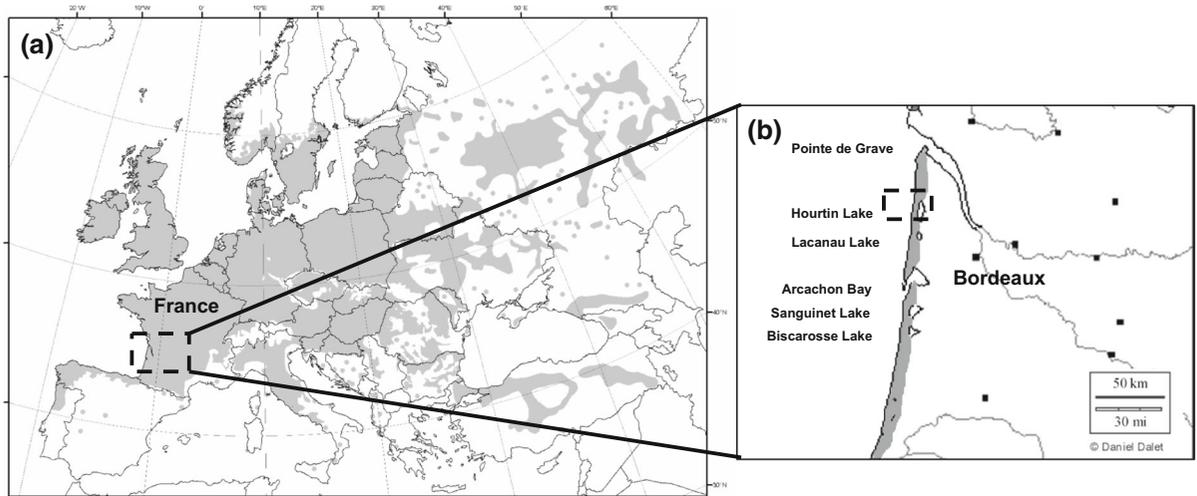


Fig. 1 Location of the experimental field. **a** Simplified map of Europe presenting the distribution range of *Q. robur* (gray area) and the general area (dashed box) where the study was conducted in South-West of France. The map is provided by EUFORGEN 2009 (www.euforgen.org). **b** The gray areas

represent the coastal dunes along the Atlantic ocean. The study was conducted in Hourtin natural reserve (dashed box). The background map was provided free of charge and use by Daniel Dalet/Académie Aix-Marseille (http://www.ac-aix-marseille.fr/pedagogie/jcms/c_67064/fr/cartotheque)

index, or process-based models generally predicted large loss of suitable habitat for *Q. robur* on the coasts of South-West France by 2055, whereas the majority of the simulations concluded that the region would remain a stable habitat for the evergreen oaks (Cheaib et al. 2012). In this area, climate scenarios predicted a warmer climate than nowadays with, for instance, an increase of 3–4 °C of mean annual temperature between the period 2071–2100 and the period 1961–1990 (SRES scenario A2, IPCC 2001). Under these scenarios we hypothesize: (i) a high risk of mortality for *Q. robur* as a response to drought events and (ii) its progressive replacement by a more prone drought-tolerant species such as holm oak (*Quercus ilex* L.). Delzon et al. (2013) indeed evidenced the colonization of *Q. ilex* along the French Atlantic coast during the last century in response to climate change. To test these hypotheses, we studied the abundance of *Q. robur* and *Q. ilex* along a gradient of water availability and their ecophysiological responses to drought.

Materials and methods

Study site

This study was conducted in the Natural Reserve of Hourtin (45°11' 14"N, 1°03'23"W, 2150 ha) located at

60 km North-east of the city of Bordeaux in the Medoc area (South-western France) on the largest European dune system (Fig. 1a, b). The two highest dunes are covered by coastal forests dominated by seeded *Pinus pinaster* Ait., with a second story of two natural co-occurring oaks, *Quercus ilex* L. and *Quercus robur* L. These forests are located at the south-western (warmer) limit of the distribution range of *Q. robur* (Fig. 1a). The understory presented an original association of Atlantic and Mediterranean species with, for instance, *Ilex aquifolium*, *Arbustus unedo*, *Castanea sativa*, *Ruscus aculeatus*, *Calluna vulgaris*, or *Erica cinerea*.

The climate of South-West France is a typical maritime Atlantic climate with cool wet winters and warm dry summers. Over the period 2000–2011, the annual temperature at Cestas near Bordeaux, France was 12.8 °C and mean annual precipitation was 797 mm (44°44'32"N 0°46'53"W, weather station no. 33122004, INRA climatic database). The proximity to the ocean induced lower daily oscillations of 0.5 °C than inside the lands (SIAEBVELG 2004), and annual precipitation measured on the coasts was linearly proportional to precipitation inside the land. Forest soils were characterized by a filtering siliceous sandy texture with more than 95 % of coarse-grained sand and low organic content (Augusto et al. 2006).

Experimental design and field measurements

All field measurements were carried out on the highest eastern barchanoid dune: twelve experimental plots of 650 m² were settled in mature Maritime pine stands (between 60 and 80 years of age) along four transects perpendicular to the dune. Three plots per transect were selected to cover a supposed increasing water stress gradient from the bottom to the top of the dune. Plot area and altitude were determined using a metric GPS device (Trimble, GéoExplorer CE séries, Sunnyvale, California). The altitude of the surface of two ponds located at the bottom of the dune close to two experimental transects and distant from one another by about 2,300 meters was determined using the same GPS device. The surface of the ponds was considered as a natural gauge of the piezometric surface of the water table. We assumed that the piezometric surface of the water table could be assimilated to a plane surface of the same altitude below the sandy dune; thus, for each plot, depth of the water table was defined as the difference between the altitude of the plot and the altitude of the piezometric surface of the water table.

In January 2008, total tree density (trees ha⁻¹) was determined on each plot by counting all trees (*Q. ilex*, *Q. robur*, *Pinus pinaster*, *Castanea sativa*, *Arbustus unedo*, and *Ilex aquifolium*) whose height was greater than 1.5 m. For each species and plot, the species relative abundance was estimated as the ratio of each tree species density to total tree density. Abundance of the regeneration was determined by counting all seedlings (height < 50 cm) and saplings (50 < height < 1.50 cm) along two 70 m transects per plot. Counting was performed according to a systematic sampling every meter along each transect (140 samplings points per plot). For each species, relative abundance of the regeneration was estimated as the ratio of the species regeneration abundance to the total regeneration abundance.

Ecophysiological data were obtained during three campaigns in May 2008, August 2008, and August 2011 on 10–20 adult trees per campaign and species (*Q. ilex* and *Q. robur*) during two consecutive days presenting similar climatic conditions (clear and sunny sky). Leaf water potential (Ψ_l , MPa) measurements were performed on 1–6 leaves per tree from predawn to midday (6:00 am to 15:30 pm) using two Scholander pressure chambers (Precis2000,

Gradignan, France and PMS Model 1000, Albany, USA). Predawn leaf water potential (Ψ_p , MPa) corresponded to the mean value of the measurements performed before sunrise and seasonal minimum leaf water potential (Ψ_m , MPa) corresponded to the mean value of the measurements inferior to -2.5 MPa. Stomatal conductance (g_s , mmol m⁻² s⁻¹) was measured on 1–6 leaves per tree between 7:30 am and 15:45 pm using a portable open system with an infrared gas analyser (CIRAS II, PP-Systems, Amesbury, MA, USA). Photosynthetically active radiation and CO₂ mixing ratio in the leaf chamber were set to 1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 380 ppm, respectively. Temperature and relative humidity in the measurement cuvette were set to track the instantaneous ambient air conditions. Vapor pressure deficit (D , Pa) was computed from those measurements.

Annual mean precipitation measured at a nearby permanent weather station (Cestas, 44°44'32"N 0°46'53"W, weather station no. 33122004, INRA climatic database) showed that 2008 was one of the wettest years since 2000, whereas 2011 was the driest one over the same period. Moreover, differences between annual precipitation and annual potential evapotranspiration calculated with the Turc equations (Turc 1961) showed a water surplus and a water deficit in 2008 and 2011, respectively (Fig. S1). Therefore, these two years will be subsequently referred to as wet (2008) and dry (2011) years.

Hydraulic traits

Vulnerability curves (VC) for *Q. ilex* and *Q. robur* were used to estimate hydraulics parameters (Fig. S2 and for details see Urli et al. 2013). For each species, a sigmoid function (Pammenter and Vander Willigen 1998) was fitted (proc NLIN, SAS version 9.2 SAS Institute, Cary NC, USA) to the VC to estimate xylem pressure inducing 50 % loss of conductance P_{50} (MPa). Xylem pressures inducing 12 and 88 % of loss of conductance (P_{12} and P_{88} , respectively, MPa) were calculated following the equations of Domec and Gartner (2001). For each species and water conditions, predicted native percent loss of conductance (PLC_p , %) was estimated using the vulnerability curves as the percent loss of conductance induced by the minimum water potential measured in the field. Hydraulic safety margins were estimated per species following Meinzer et al. (2009): the differences were calculated between

the minimum water potential (Ψ_m) experienced during the dry year and the water potential inducing either 12, 50, and 88 % loss of conductance $\Psi_m - P_{12}$, $\Psi_m - P_{50}$, and $\Psi_m - P_{88}$ (MPa).

Statistical analyses

Non-linear regressions of relative abundance per species on depth of the water table were fitted (PROC NLIN, SAS version 9.2 SAS Institute, Cary NC, USA). Differences in Ψ_l , Ψ_m and PLC_p between species and water conditions (wet and dry years) were tested using two-way analyses of variance and post hoc multiple mean comparisons were tested with Bonferroni tests (PROC GLM, SAS version 9.2 SAS Institute, Cary NC, USA). Differences in hydraulic safety margins between species were tested using t test analyses (PROC TTEST, SAS version 9.2 SAS Institute, Cary NC, USA). The relationship between g_s and D was fitted (PROC GLM, SAS version 9.2 SAS Institute, Cary NC, USA) using the equation of Oren et al. (1999):

$$g_s = -m \cdot \ln D + b, \quad (1)$$

where m represents the sensitivity of g_s to D and b a reference conductance at $D = 1,000$ Pa

Analysis of covariance with repeated measurements (PROC MIXED, SAS version 9.2 SAS Institute, Cary NC, USA) was performed to test the differences in stomatal control in response to vapor pressure deficit between species with $\ln D$ as the regressor and species as the categorical variable.

Results

Local species distribution and depth of the water table

Tree density varied from 2,318 to 13,412 trees.ha⁻¹ for *Q. ilex* and from 79 to 1,362 trees.ha⁻¹ for *Q. robur*. Abundance of the regeneration varied from 2 to 32 % for *Q. ilex* and from 0 to 4 % for *Q. robur*. Relative abundance of both adult trees and regeneration was higher for *Q. ilex* compared to *Q. robur* for all plots except one. Species relative abundance was highly dependent on the depth of the water table: with increasing depth of the water table, the relative abundance of adult *Q. robur* decreased gradually from 65 to 0 % (non-linear regression, $P = 0.0002$),

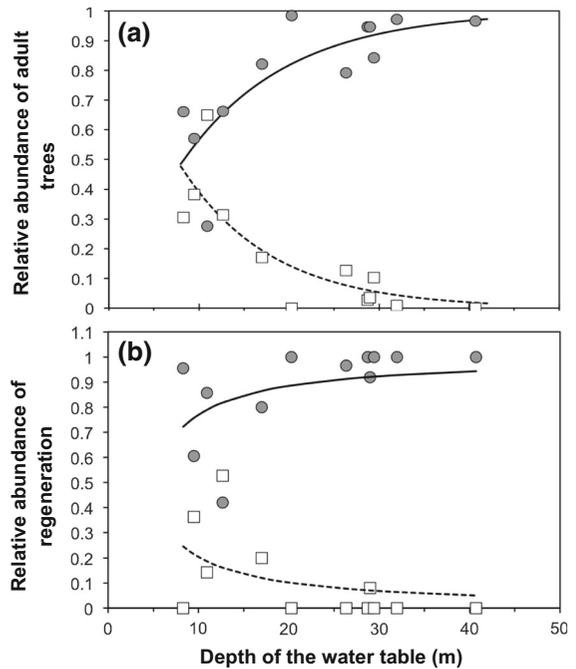


Fig. 2 Relationships between the relative abundance of adult trees (a) and regeneration (b) and the depth of the water table for *Q. robur* (white squares, dashed line) and *Q. ilex* (gray circles, black line). Each point corresponds to one sample plot and lines to the fitted model per species: adult *Q. ilex* $y = 1 - 0.08643e^{(-0.08643(x-28.65878))}$, $P < 0.0001$; adult *Q. robur* $y = 0.09974e^{(-0.09974(x-23.6849))}$, $P = 0.0002$; regeneration *Q. ilex* $y = 1 - \frac{2.3064}{x}$, $P < 0.0001$; regeneration *Q. robur* $y = \frac{2.0383}{x}$, $P = 0.0108$

whereas that of adult *Q. ilex* increased (non-linear regression, $P < 0.0001$) from 28 to 98 % (Fig. 2a). We observed the same trend for relative abundance of the regeneration; the pattern was even more abrupt with an absence of regeneration of *Q. robur* and an almost complete domination of *Q. ilex* where the water table was the deepest (Fig. 2b, non-linear regression, $P = 0.0108$ and $P < 0.0001$ for *Q. robur* and *Q. ilex*, respectively). *Q. ilex* was present on the dune whatever the elevation, whereas *Q. robur* was almost absent at the top of the dune.

Leaf water potentials

Both species had significantly lower values of pre-dawn water potential Ψ_p during the dry year compared to the wet year (water effect, Fig. 3a, Table 1). During the dry year, we found a more negative Ψ_p for *Q. ilex* compared to *Q. robur*, whereas no differences were observed between species during the wet year (species

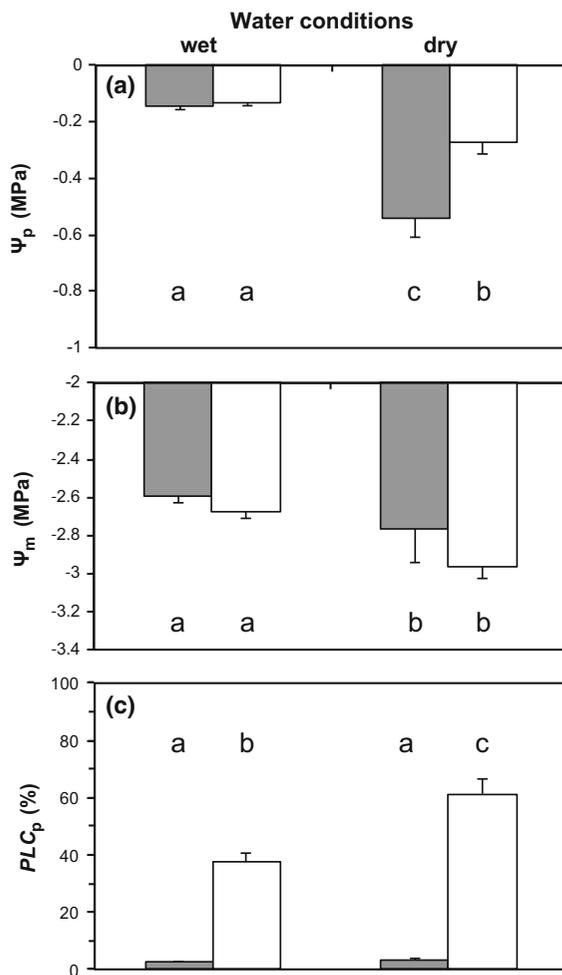


Fig. 3 **a** Predawn leaf water potential (Ψ_p , MPa), **b** seasonal minimum leaf water potential experienced during the summer period (Ψ_m , MPa) and **c** predicted native PLC (PLC_p , %) for both oaks: *Q. ilex* (gray bars) and *Q. robur* (white bars) under two water conditions: wet year (2008) and dry year (2011). $n \geq 5 \pm$ S.E. Means with the same letters are not significantly different ($\alpha = 0.05$)

and species \times water effects, Fig. 3a, Table 1). Seasonal minimum water potential experienced during the summer period was lower during the dry year (water effect, Fig. 3b, Table 1), but no significant differences were observed between species whatever the water conditions (neither species nor interaction effects, Fig. 3b; Table 1).

Hydraulic traits

The values of xylem pressure inducing 12, 50, and 88 % of loss of conductance (P_{12} , P_{50} and P_{88}) were

−3.95, −5.52, and −7.08 MPa and −2.25, −2.83, and −3.41 MPa for *Q. ilex* and *Q. robur*, respectively (Urli et al. 2013, Fig. S2). As a result of these differences in vulnerability to cavitation between species, predicted native PLC (PLC_p) was significantly different between species (Fig. 3c; Table 1): a high PLC_p was estimated for *Q. robur* (37.69 ± 2.63 % and 61.32 ± 4.93 % during the wet year and the dry one, respectively), whereas PLC_p of *Q. ilex* was lower whatever the water conditions (2.36 ± 0.09 and 3.22 ± 0.86 % during the wet year and the dry one, respectively). Moreover, PLC_p of *Q. robur* significantly increased with dryness, whereas no difference was observed for *Q. ilex* between the two water conditions (dry and wet years) (interaction effect, Fig. 3c; Table 1).

Whatever the level of water stress used to estimate the hydraulic safety margins (P_{12} , P_{50} , P_{88}), it was higher for *Q. ilex* compared to *Q. robur* (Fig. 4; Table 2). The safety margin $\Psi_m - P_{88}$ was below 1 MPa and close to 0 for *Q. robur* contrary to *Q. ilex* (Fig. 4), which exhibited high safety margins (over 4 MPa). Moreover, $\Psi_m - P_{12}$ corresponded to negative values for *Q. robur*, whereas it remained positive for *Q. ilex* (Fig. 4). Values of safety margins defined with P_{50} were always positive for *Q. ilex*, whereas $\Psi_m - P_{50}$ presented null values for *Q. robur* (Fig. 4).

Stomatal control

Stomatal conductance decreased with increasing vapor pressure deficit (regressor $\ln D$ in the ANCOVA, $F_{1-83} = 68.38$, $P < 0.0001$, Fig. 5) for both species. The reference conductance at $D = 1,000$ Pa was significantly higher for *Q. robur* ($b = 570.33$) than for *Q. ilex* ($b = 407.80$) (species effect in ANCOVA, $F_{1-83} = 4.86$, $P = 0.0302$, Fig. 5) as well as the sensitivity of its stomatal response to D (*Q. ilex* $m = 42.86$ and *Q. robur* $m = 63.09$; interaction effect, $F_{1-83} = 4.33$, $P = 0.0405$, Fig. 5).

Discussion

The abundance of oaks was highly correlated with water availability in this coastal forest located at the southern edge of the distribution of *Q. robur*. Both oak species presented different hydraulic strategies: *Q. ilex* is more resistant to cavitation than *Q. robur*. Because the minimum water potential did not differ between

Table 1 Two-way ANOVA results of predawn (Ψ_p , MPa) and seasonal minimum (Ψ_m , MPa) water potentials, predicted native embolism (PLC_p , %) between both oaks (*Q. ilex* and *Q.*

robur) under different water conditions (dry vs. wet). Bold values indicate significant effects ($P < 0.05$)

	Ψ_p				Ψ_m				PLC_p			
	SS	df	F	P	SS	df	F	P	SS	df	F	P
Species	0.293	1-67	27.19	$<10^{-4}$	0.123	1-22	3.33	0.0817	13758.95	1-22	292.93	$<10^{-4}$
Water	1.014	1-67	94.10	$<10^{-4}$	0.329	1-22	8.87	0.0069	945.28	1-22	20.13	2×10^{-4}
Species x Water	0.240	1-67	22.31	$<10^{-4}$	0.021	1-22	0.57	0.4565	817.17	1-22	17.40	4×10^{-4}

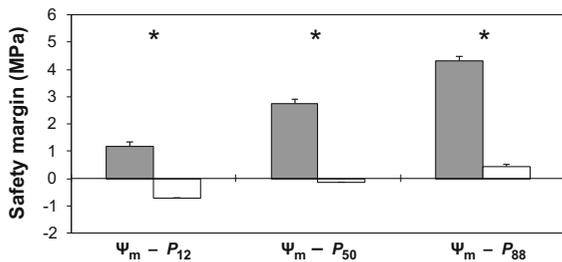


Fig. 4 Hydraulic safety margin calculated for three levels of water stress as the difference between minimum water potential (Ψ_m , MPa) during the dry year and potential inducing 12 % (P_{12} , MPa), 50 % (P_{50} , MPa), and 88 % (P_{88} , MPa) loss of conductance for both oaks: *Q. ilex* (gray bars) and *Q. robur* (white bars). $n \geq 5 \pm S.E.$ Asterisks showed significant differences ($\alpha = 0.05$) in hydraulic safety margin between species

species during drought conditions, the hydraulic safety margin was much higher for *Q. ilex* than *Q. robur*. The latter functioned very closely to pressure inducing 88 % of xylem cavitation (P_{88}), which is known to lead to death in angiosperm seedlings (Barigah et al. 2013; Urli et al. 2013). Therefore, in the current context of climate change and increasing severe drought (Burke et al. 2006; Jentsch et al. 2007), mortality of *Q. robur* should increase while *Q. ilex* should persist and spread in the coastal dune forests of South-West France.

Strong decline in *Q. robur* abundance with increasing water stress

Overall, tree density and relative abundance of *Q. robur* were low compared to those of *Q. ilex*. Indeed, *Q. robur* is mostly present at the bottom of the dunes where water is more readily available (lower depth of the water table), and several diebacks of mature trees of *Q. robur* located in the slopes or the top of the dune were observed (ONF 2010 and personal observations). Since the end of the 19th century, *Q. ilex* colonized this area (Delzon et al. 2013) and nowadays constitutes the most abundant tree species in this forest with higher relative abundance (close to 100 %) at the top of the dune.

The regeneration patterns suggest how expected increasing drought may impact these forests. Indeed, seedling is the woody plant life form presenting the highest mortality rates (Leck and Outred 2008) as a consequence of their high vulnerability to herbivory, pathogens, and drought (e.g., Cui and Smith 1991; Davis et al. 1999; Negussie et al. 2008). Sanchez-Gomez et al. (2006) showed that seedling mortality was higher for *Q. robur* than for *Q. ilex* during water stress under cover: *Q. ilex* seedling survival rate remained close to 95 % during 40 days of water stress, whereas *Q. robur* seedling survival rates dropped

Table 2 T-test results of three types of hydraulic safety margins ($\Psi_m - P_{88}$, $\Psi_m - P_{50}$, and $\Psi_m - P_{12}$, MPa) experienced during the dry year between both oaks (*Q. ilex* and *Q. robur*). ($P < 0.05$ is considered as statistically significant)

	$\Psi_m - P_{12}$			$\Psi_m - P_{50}$			$\Psi_m - P_{88}$		
	df	t	P	df	t	P	df	t	P
Species	9	11.09	$<10^{-4}$	9	16.88	$<10^{-4}$	9	22.61	$<10^{-4}$

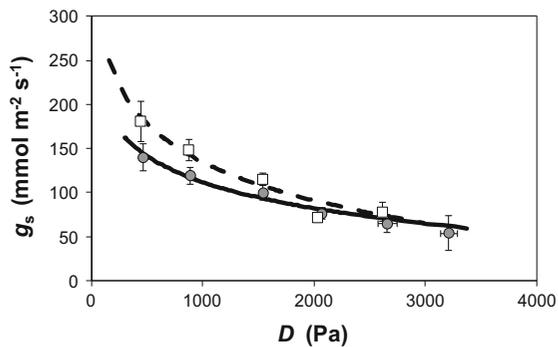


Fig. 5 Stomatal conductance (g_s , $\text{mmol m}^{-2} \text{s}^{-1}$) response to increasing vapor pressure deficit (D , Pa) for *Q. ilex* (gray circles, black line) and for *Q. robur* (white squares, dashed line). Each point represents the mean value (\pm S.E) of at least 4–42 stomatal conductance measurements as a function of the mean value (\pm S.E) of D , over six classes of 600 Pa. Lines represent g_s fitted according to the following equations: $g_s = -42.86 \ln D + 407.80$, $P < 0.0001$, and $g_s = -63.09 \ln D + 570.33$, $P < 0.0001$, for *Q. ilex* and *Q. robur*, respectively

down to 50 % after 10 days of water stress (soil water content of 7 %). Such sensitivity, together with the lower presence of mature adult trees under the more water-stressed habitats (top of the dunes), could explain the quasi-absence of regeneration for *Q. robur* compared to the high level of regeneration that we observed for *Q. ilex*. This suggests that these coastal forests will be likely dominated by *Q. ilex*.

Hydraulic strategies and consequences for responses to water stress

Q. robur experienced higher native embolism in the field ($PLC_p = 50\%$) compared to *Q. ilex* ($PLC_p < 5\%$), despite similar minimum predawn and minimum water potentials between species. These differences in level of native embolism between species are explained by high differences in cavitation resistance (Cochard et al. 1992; Urli et al. 2013) and not by differences in stomatal regulation between oaks. Through stomatal regulation, plants can control water loss and keep their xylem water potential above the cavitation threshold, thus preserving the integrity of their vascular apparatus (Cochard et al. 1996; Tognetti et al. 1998; Oren et al. 1999; Martinez-Vilalta et al. 2003). However, although *Q. robur* showed a slightly higher stomatal sensitivity to vapor pressure deficit than *Q. ilex*, stomatal conductance of both

species was very close at high values of D . This stomatal regulation in response to D or soil water stress during summer drought was well known for *Q. ilex* (Tognetti et al. 1998; Martinez-Vilalta et al. 2003; David et al. 2007; Quero et al. 2011) and *Q. robur* (Breda et al. 1993; Triboulot et al. 1996; Morecroft and Roberts 1999). Although *Q. ilex* and *Q. robur* both presented a mechanism of drought avoidance due to stomatal regulation, *Q. ilex* was more water stress resistant due to a higher cavitation resistance than *Q. robur*. Moreover, during extreme drought, plant and leaf mortality occurred at lower water potential values for *Q. ilex* than for *Q. robur* due to their differences in cavitation resistance (Urli et al. 2013). Thus, *Q. robur* can be considered as a typical isohydric species, whereas *Q. ilex* presented an intermediate strategy between anisohydry and isohydry (Limousin et al. 2009).

Q. ilex was already known to be a cavitation resistant diffuse-porous oak (Tyree and Cochard 1996; Quero et al. 2011). By comparison, *Q. robur* is one of the most cavitation sensitive ring-porous oaks (Cochard et al. 1992; Breda et al. 1993). The mechanisms underlying the relationship between cavitation resistance and xylem anatomy (wood density, vessel size, intervessel pit structure, membrane thickness and porosity) are currently highly debated (Hajek et al. 2014). However, some of these characteristics could explain the differences in cavitation resistance between both oaks. Several studies showed that lower vulnerability to drought and/or cavitation was associated with larger wood density (Hacke and Sperry 2001, Jacobsen et al. 2007, Pratt et al. 2007). This is in accordance with the higher wood density of *Q. ilex* compared to that of *Q. robur* (0.82 and 0.575 g cm^{-3} , respectively, Zanne et al. 2009). The correlation between high wood density and high cavitation resistance in Mediterranean plants could be explained by the necessity for plants experiencing low values of water potential to reinforce their vessel walls to avoid cell implosion before suffering from embolism (Hacke and Sperry 2001, Nardini et al. 2014).

These contrasting hydraulic strategies impacted plant functioning in the field. Stomatal regulation of *Q. ilex* allowed the maintenance of a large positive safety margin relative to the minimum water potential inducing 12 % of loss of conductance ($\Psi_m - P_{12}$). We can conclude that soil water availability in the dunes even during the drier year allowed *Q. ilex* to

maintain a fully functional hydraulic system (Domec and Gartner 2001; Meinzer et al. 2009). By comparison, the water stress experienced by *Q. robur* corresponded to a negative safety margin ($\Psi_m - P_{12}$). At $\Psi_m < P_{12}$, a low increase of xylem pressure dramatically increases the risk of runaway embolism (Meinzer et al. 2009). Thus, the drought experienced in the field during our study corresponded to a more severe water stress for *Q. robur* compared to *Q. ilex*. Moreover, *Q. ilex* kept high safety margins relative to 50 % and 88 % of loss of conductance ($\Psi_m - P_{50}$, $\Psi_m - P_{88}$), whereas those of *Q. robur* were negative or close to 0: *Q. robur*, thus functioned very closely to the cavitation threshold inducing plant death. Indeed, these thresholds of 50 or 88 % of loss of conductance are more relevant to define the hydraulic safety margin under more severe drought and thus to assess the risk of species mortality in the field: P_{50} corresponds to cavitation inducing leaf shedding and branch dieback (Meinzer et al. 2009), and P_{88} corresponds to a level of cavitation generally inducing plant death in angiosperm tree species (Barigah et al. 2013, Urli et al. 2013). All together considering *Q. robur* narrow safety margins and high vulnerability to cavitation, these results suggest that the increasing frequency of extreme drought events that is expected in the future (Burke et al. 2006; Jentsch et al. 2007) should highly impact the functioning and survival of this species in South-West France at its warmer margin. On the contrary, *Q. ilex* should be able to cope with increasing water stress considering the low vulnerability of its hydraulic system and it should outcompete *Q. robur* in these areas.

Conclusions

The novelty of our work is the use of hydraulic safety margin coupled with demography measurements to assess the mortality risks of a tree species located at the southern edge of its distribution range and its potential replacement. We showed that *Q. robur* presented narrow hydraulic safety margins that could threaten its survival in the context of climate change, which predicts increasing drought. On the contrary, *Q. ilex* should be able to cope with higher water stress because of its higher cavitation resistance; this should favor *Q. ilex* in the future as already observed by the quasi-absence of *Q. robur* regeneration. Our

methodology should be transferable to the analysis of other species and could be a useful tool for the study of impacts of increasing drought from local to regional scales.

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