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Original article

Response of Scots pine (*Pinus sylvestris* L.) and pubescent oak (*Quercus pubescens* Willd.) to soil and atmospheric water deficits under Mediterranean mountain climate

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Abstract – The physiological responses to water deficits of Scots pine (*Pinus sylvestris* L.) and pubescent oak (*Quercus pubescens* Willd.) were studied under Mediterranean mountain climate. Minimum leaf water potentials were −3.2 MPa for oak and −2.1 MPa for pine, with higher predawn values for pubescent oak. Relative sap flow declined in both species when vapour pressure deficit (D) went above ca. 1.2 kPa, but stomatal control was stronger for pine during the 2003 summer drought. *P. sylvestris* plant hydraulic conductance on a half-total leaf area basis ($k_{L,s-l}$) was 1.2–2.6 times higher than the values shown by *Q. pubescens*, and it showed a considerably steeper decrease during summer. Leaf-level gas exchange was positively related to $k_{L,s-l}$ in both species. Scots pine was more vulnerable to xylem embolism and closed stomata to prevent substantial conductivity losses. The results of this study confirm that pubescent oak is more resistant to extreme drought events.

canopy stomatal conductance / drought / hydraulic conductance / Mediterranean climate / sap flow

Résumé – Réponses du pin sylvestre (*Pinus sylvestris* L.) et du chêne pubescent (*Quercus pubescens* Wild.) aux déficits hydriques atmosphérique et édaphique sous climat montagnard méditerranéen. Les réponses physiologiques aux déficits hydriques du pin sylvestre (*Pinus sylvestris* L.) et du chêne pubescent (*Quercus pubescens* Wild.) ont été étudiées sous climat montagnard méditerranéen. Le potentiel hydrique foliaire minimum atteint a été de −3,2 MPa pour le chêne et de −2,1 MPa pour le pin, avec des valeurs de potentiel de base plus élevées pour le chêne pubescent. Un relatif déclin du flux de sève a été observé chez les deux espèces lorsque le déficit de vapeur d'eau dépassait 1,2 kPa, mais le contrôle stomatique a été plus fort chez le pin pendant la sécheresse de l'été 2003. La conductance hydraulique des pins, ramenée à la surface foliaire ($\mathrm{k}_{\mathrm{L,s-1}}$) a été de 1,2 à 2,6 fois plus élevée que celle de *Quercus pubescens* et a présenté une rapide décroissance pendant l'été. Le niveau des échanges gazeux foliaires était positivement corrélé à $\mathrm{k}_{\mathrm{L,s-1}}$ chez les deux espèces. Le pin sylvestre est plus vulnérable à l'embolie du xylème et a de ce fait fermé ses stomates pour empêcher une perte substantielle de conductivité hydraulique. Les résultats de cette étude confirment que le chêne pubescent est plus résistant aux épisodes d'extrême sécheresse que le pin sylvestre.

conductance stomatique du couvert / sècheresse / conductance hydraulique / climat méditerranéen / flux de sève

1. INTRODUCTION

Scots pine (*Pinus sylvestris* L.) and pubescent oak (*Quercus pubescens* Willd.) are two of the most representative tree species in mountain areas of NE Spain. While Scots pine is a Eurosiberian species with a broad distribution, pubescent oak, restricted to southern Europe, occupies the transition zone between Mediterranean-type and more humid environments [23].

Although both species coexist, they differ in the main morphological traits of the water transport pathway from roots to leaves. Scots pine is an evergreen conifer, with tracheid-bearing xylem and pubescent oak is a winter deciduous or marcescent broadleaved species, with ring-porous xylem. Due to its tracheid xylem anatomy, Scots pine shows a very low sapwood conductivity, as generally observed in conifers [34], but it also has very low leaf-to-sapwood area ratios (A_L:A_S) compared to other pine species [15]. The contrary usually holds for deciduous oak species, which show higher efficiency of the conducting elements and higher A_L:A_S [46]. These contrasting combinations of traits may result in a similar hydraulic sufficiency at the whole-plant level [3].

With regard to water economy strategies, Scots pine closes stomata when soil moisture deficit has reached a specific threshold [22] whereas pubescent oak maintains high transpiration rates despite the incidence of drought [32], partly due to the ability to extract water from deep soil layers and groundwater [45]. While Scots pine is relatively vulnerable to embolism [11], and accordingly, shows a tight stomatal control [22] published studies suggest a comparatively less tight control in *Q. pubescens* [14].

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Trees adjust their transpiration rates to the capacity of the hydraulic system to supply canopy leaves with water by means of a close coordination between hydraulic and stomatal conductance, which can result in similar responses to environmental conditions across co-existing species [30]. Recent studies on co-occurring Scots pine and pubescent oak have shown slightly higher water deficits in the former species [49]. Indeed, there is increasing evidence that extreme drought episodes affect Scots pine particularly [28], while deciduous oaks like for instance *Quercus petraea* (Matt.) Liebl., seem unaffected [26].

In this study we compare the physiological response of these two species under the Mediterranean mountain climate coexisting under the Mediterranean mountain climate of the Eastern Pyrenees. Particularly, the aims of our study were: (1) to find whether *P. sylvestris* shows a tighter stomatal control under limiting conditions of water supply, (2) to investigate differences in stomatal dynamics and its relation to water potential and hydraulic conductance across both species, and (3) to examine the relevance of stomatal control of xylem embolism, especially in *P. sylvestris*, given the importance of this species in Mediterranean mountain landscapes.

2. MATERIAL AND METHODS

2.1. Study sites

The two experimental plots are part of the Vallcebre research area (42° 12' N, 1° 49' E), located in the Eastern Pyrenees (NE Spain). Climate is sub-Mediterranean, with an average air temperature of 7.3 °C (measured at 1440 m.a.s.l.) and 924 mm of annual rainfall [16]. The present landscape is mainly a mosaic of mesophilous grassland of the *Aphyllantion* type and Scots pine forests, which colonised old agricultural terraces after their abandonment [37]. The extension of pubescent oak forests in the area has been reduced to small patches in unfavourable locations, although it is frequent to find *Q. pubescens* saplings in the undergrowth of Scots pine stands [13].

The Scots pine plot is located in an abandoned terraced slope, at an elevation of *ca.* 1260 m.a.s.l. The understorey is scarce, mainly scattered *Buxus sempervirens* L. shrubs and a discontinuous herb layer. Stand density and basal area are 2165 trees ha^{-1} and 44.7 m^2 ha^{-1}, respectively. Mean diameter (±SE) at breast height (DBH) is 15.0 ± 0.7 cm and projected leaf area index (LAI) is 2.4 m^2 m^{-2}. Mudstone and sandstone are the principal underlying lithologies, originating sandy-loam soils about 65 cm deep (Rubio, unpublished results).

The oak plot is located just 0.8 km apart from the pine plot, and it is characterised by a lower tree density (828 trees ha^{-1}), lower LAI (2.1 m^2 m^{-2}), and the presence of a dense and species-rich understorey with other tree (*Prunus avium* L., *Fraxinus excelsior* L., *Acer campestre* L.) and shrub species (*Buxus sempervirens* L., *Prunus spinosa* L., *Rubus* spp. and *Rosa* spp.). Trees are larger than in the pine plot (mean tree diameter of 21.1 ± 1.4 cm), but oak basal area, which represents 99% of total tree basal area, is lower (32.5 m^2 ha^{-1}). The upper soil, which is formed by a loamy matrix and limestone blocks, is about 50 cm deep [39].

2.2. Meteorological and soil moisture measurements

Above-canopy meteorology, soil moisture and sap flow were measured continuously between May 2003 and August 2005. Detailed information on the meteorological monitoring can be found in recent publications about research carried out in the same experimental plots [36].

Soil moisture in the top 30 cm was measured continuously with vertically installed water content reflectometers (CS615-CS616, Campbell Scientific, Leicester, Leicestershire, UK). Both probes were calibrated using weekly measurements of soil water content with the TDR technique (Tektronix 1502C, Beaverton, Oregon, USA) in the vicinity of the reflectometer, and corrected for soil temperature effects. Weekly manual measurements of soil moisture began in June 2003 in both plots, whereas continuous monitoring began in June 2003 in the pine plot and May 2004 in the oak plot. To account for the spatial variability of soil moisture the output from both reflectometers was related to an average weekly measurement of soil moisture in each plot, obtained from 4 and 5 TDR probes located randomly in the pine and the oak plots, respectively. The resulting linear relationships were used to estimate an average soil moisture value for each stand. Additional soil moisture measurements were taken with two vertically placed TDR probes at deeper locations in the soil (30–60 cm in the pine plot and 30-50 cm in the oak plot, respectively).

A water retention curve was constructed from 2–3 unaltered soil samples at each depth interval (0–5 cm, 5–10 cm, 10–15 cm and 25–30 cm deep), in both monitored plots. Volumetric moisture of soil samples was measured at matric potentials of −0.25 kPa, −1 kPa and −3.2 kPa using the sand-box method, and at −0.1 MPa, −0.32 MPa and −1.5 MPa using the pressure membrane method [38]. These detailed data were primarily obtained for a parallel investigation on the differences in soil hydraulic properties related to changes in land cover (Rubio 2005). However, here we were interested in converting our soil moisture measurements in the upper 0–30 cm into soil water potentials averaged over the same depth ($\psi_{s,0-30}$) using soil water retention curves. Therefore we obtained only one curve for each plot calculating first the depth-averaged value of soil moisture at the given suction for the upper 30 cm (e.g. samples at 10–15 cm and 25–30 cm were assumed to be representative of the 15–20 cm and 20–25 cm intervals, respectively). For simplicity, we used the retention curve whose mathematical form fitted best the data, (nonlinear regression, SPSS v.13.0, Chicago, USA), and not a more physically-based model [47].

2.3. Sap flow

In each plot, sap flow was measured with heat dissipation probes [17] manufactured in our lab. Sap flow gauges were installed at breast height, and covered with reflective insulation to avoid the influence of natural temperature gradients in the trunk. A maximum of 12 trees was measured simultaneously (Tab. I). Probes installed in pines were 20 mm long, whereas those used in oaks were 10 mm to minimize the errors due to steep gradients in sap flow density along the depth of the sensor [8].

Sap flow measured by Granier sensors was corrected for radial variability in sap flow density as done previously for pubescent oak [36]. Briefly, a multi-point Heat Field Deformation sap flow sensor [31] was used to measure sap flow at five depths and relate the value of sap flux density at each depth to a reference sap flow equivalent to sap flux density measured by the Granier sensor. Then,

Table I. Trees and periods of sap flow measurements: long-term monitoring with heat dissipation (HD) sensors and radial patterns measurements with heat field deformation (HFD) sensors.

	Tree ID	DBH (cm)	Height (m)	Period of HD sap flow measurements	Period of radial patterns measurements
P. sylvestris	1	6.7	6.3	May 2004–Aug 2005	
	2	10.2	11.0	Jun 2003–Aug 2005	
	3	11.3	10.5	May 2004–Aug2005	
	4	12.7	10.5	May 2004–Aug 2005	217-220 (5–8 Aug)*
	5	13.3	10.5	May 2004–Aug2005	
	6	15.9	10.5	Jun2003–Aug 2005	203-216 (22 Jul–4 Aug)
	7	18.0	9.5	May 2004–Aug 2005	196-203 (15–22 Jul)*
	8	19.4	13.0	Jun 2003–Mar 2004	
	9	19.9	12.5	Jun 2003–Aug 2005	
	10	20.4	12.5	Jun 2003–Aug 2005	102-110 (2–10 Apr)*
	11	22.5	12.5	May 2004–Aug 2005	181-186 (30 Jun–5 Jul)*
	12	27.9	12.5	Jun 2003–Aug 2005	116-120 (26–30 Apr)*
	13	29.3	11.5	May 2004–Aug2005	173-181 (22–30 Jun)*
Q. pubescens	1	8.7	7.2	May 2003–Oct 2004	197-199 (15–17 Jun)**
	2	12.6	9.1	May 2003–Sept 2004	
	3	14.5	10.0	May 2003–Aug 2004	
	4	17.85	10.9	May 2003–Aug 2005	203-206 (21–24 Jul)**
	5	19.2	11.2	May 2003–Nov 2004	
	6	20.9	10.5	May 2003–Aug 2005	279-281 (5–7 Oct)**
	7	21.1	11.7	May 2003–Aug 2005	265-267 (21–23 Sep)**
	8	21.5	11.8	May 2003–Oct 2004	272-275 (28 Sep–1Oct)**
	9	26.2	10.0	May 2003–Aug 2005	233-235 (20–22 Sep)**
	10	26.7	14.0	May 2003–Sept 2004	277-279 (3–5 Oct)**
	11	34.5	10.0	May 2003–Sept 2004	269-270 (25–26 Sep)**
	12	38.2	13.0	May 2003–Sept 2004	200-202 (18–20 Jul)**

* Year 2005; ** Year 2004.

a whole-tree correction coefficient was obtained dividing total sap flow, obtained by adding up sap flow in individual sapwood annuli, by sap flow calculated considering a uniform density profile.

Tree sap flow and leaf gas exchange (see below) were related to half-total leaf area in order to compare both species. To convert *P. sylvestris* projected leaf area to half-total leaf area we multiplied the former by a coefficient of 1.35 [40]. Given that the main purpose of our study was to identify the different responses to varying environmental conditions of pines and oaks, we normalised sap flow per unit leaf area at midday ($Q_{\mathrm{L,md}}$) with respect to its maximum value [26]. Relative sap flow at midday was then related to vapour pressure deficit (D), net radiation (R_{n}) and soil moisture deficit SMD, calculated from maximum and minimum values of soil moisture ($\theta_{\max}$, $\theta_{\min}$) [18]:

$$SMD = \frac{\theta_{\max} - \theta}{\theta_{\max} - \theta_{\min}}. \quad (1)$$

We also calculated canopy stomatal conductance at midday ($G_{s,md}$) derived from sap flow measurements [48], averaging the individual tree values of canopy stomatal conductance (G_s) at the 15-min time-step from 11:00 to 13:00 solar time.

2.4. Leaf-level gas exchange

Leaf stomatal conductance to water vapour (g_s) was measured in both species with a portable gas exchange system (LI-6200, LiCor Inc., NE, USA). Six to eight leaves or twigs from the lower canopy were sampled 2–4 times along the day on the 19th–20th May (only in Scots pine), 17th June, 14th–15th July, 4th and 30th August of the year 2005 (DOY 139-140, 168,194-195, 216 and 242).

2.5. Leaf water potential measurements

Predawn (2:00–4:00 h, solar time) and midday (11:00–13:00 h, solar time) water potentials were measured in both plots at one date in the year 2003 and every 2–4 weeks during the 2004 and 2005 growing seasons. For each sampling, leaves or twigs from 4–6 trees were sampled with a pruning pole reaching about 4 m high in the canopy, immediately measuring their water potential with a pressure chamber (PMS Instruments, OR, USA).

2.6. Vulnerability to embolism in *P. sylvestris* branches

Additionally, given the dominance of Scots pine forests in the study area, vulnerability to embolism was assessed for this species. A total of 10 mid-crown branches were sampled in August 2004, placed in plastic bags and taken to the lab, where they were stored at 4 °C during 2 days. Leaves were detached from the branches and their projected leaf area was measured with a leaf area meter (LI-3100, LiCor Inc., NE, USA) Vulnerability to embolism was measured using the air injection method [10]. The branches (0.6–1.1 cm in diameter) were cut under water to a final length of ca. 20 cm, and put inside a pressure

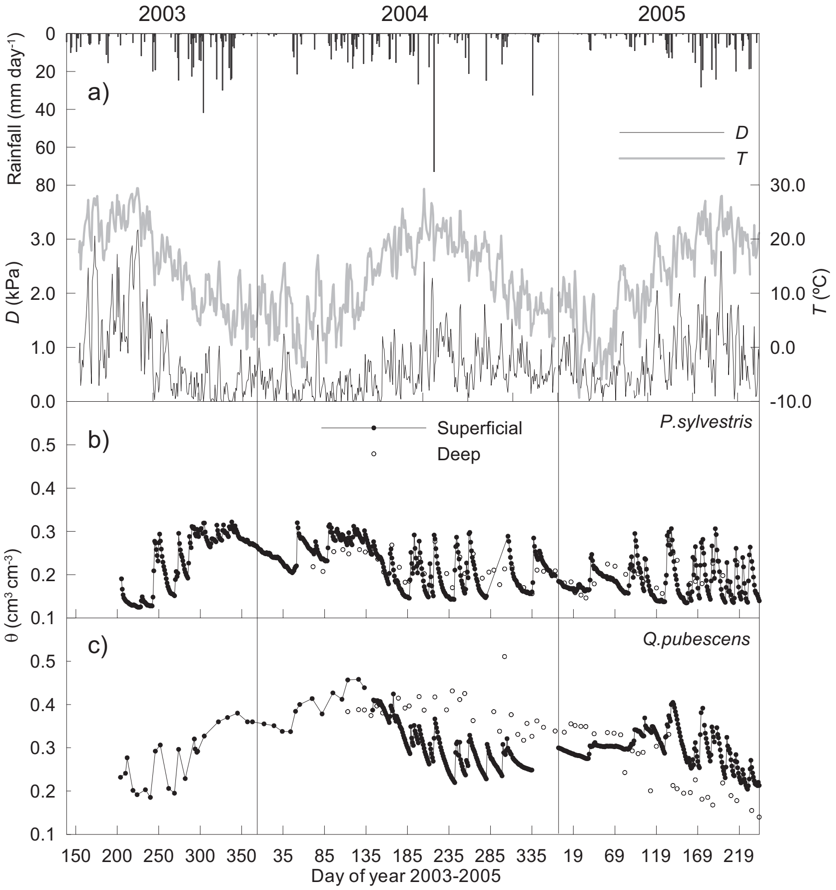

Figure 1. Meteorology and soil moisture during the whole period of study (June 2003–August 2005). (a) Air temperature (T) and vapour pressure deficit (D) only shown for the pine plot, and rainfall measured in a clearing close to the pine plot. (b, c) Closed dots represent superficial soil moisture (θ_{0-30}), measured continuously or weekly (at the beginning of the monitoring period in the oak plot). Open dots correspond to soil moisture in deeper soil layers measured weekly in both plots (θ_{30-50} in the oak plot and θ_{30-60} in the pine plot).

chamber with both ends protruding. The proximal end was connected to a tubing system filled with a filtered (Φ = 0.22 µm) and degassed solution of HCl (pH around 2). This solution was injected at a pressure of 75 kPa during 1 hour to remove all native embolisms. Then, the solution was allowed to flow from the tubing system through the branches, driven by a pressure gradient of ca. 6 kPa. Maximum hydraulic conductivity was calculated dividing the flow rate through the segment, measured gravimetrically with a previously weighed vial filled with cotton at the exposed end, by the pressure gradient. The segments were then subjected to a 1 MPa rise inside the chamber and maintained during 15 min. The system was allowed to equilibrate setting the pressure at 25 kPa for 10 min and then conductivity was measured again. We repeated this process, increasing the injection pressure 1 MPa at each step, until we reached 5 MPa.

We calculated the percent loss in conductivity (PLC), with respect to the initial measurement, for each pressure level. Vulnerability to embolism was described by the following function, fitted using non-linear least squares regression (procedure nls in R Statistical Software, v.2.0.1)

$$PLC = 100/(1 + \exp(a(\psi - b))) \tag{2}$$

where b is the pressure (MPa) causing a 50% loss of conductivity and a (MPa^{-1}) is related to the slope of the curve. This protocol also allowed us to calculate maximum wood-specific (K_W, m^2 wood area MPa^{-1} s^{-1}) and leaf-specific (K_L, m^2 leaf area MPa^{-1} s^{-1}) conductivities at the branch level from the initial conductivity values divided by branch cross-sectional area or distal leaf area, respectively.

2.7. Hydraulic conductance

Whole plant hydraulic conductance ($k_{\mathrm{L,s-l}}$, kg m^{-2} s^{-1} MPa^{-1}) was calculated from the average value of leaf-area based sap flow rates at midday, between 11:00 and 13:00 solar time ($Q_{\mathrm{L,md}}$, kg m^{-2} s^{-1}) and soil-to-leaf water potential difference (MPa):

$$k_{\mathrm{L,s-l}} = \frac{Q_{L,md}}{\psi_s - \psi_l - \rho g h} \tag{3}$$

ψ_s is soil water potential estimated from predawn leaf water potential corrected for gravity effects, ψ_l is obtained from water potential measurements at midday, g is acceleration due to gravity (m s^{-2}), ρ is water density (kg m^{-3}) and h is sampling height (m).

Table II. Rainfall during the selected periods compared to the long-term average.

	Rainfall (mm)	
	September*–May	June–August
2003	–	116.0
2004	648.0	221.0
2005	315.6	257.0
**Long-term average (1994–2002)	650.5	245.6

* Of the previous year; ** Latron et al., [25].

3. RESULTS

3.1. Meteorology and soil moisture during the study period

Meteorological conditions were very similar in both plots, therefore only the data above the pine stand is shown (Fig. 1). Maximum daytime-averaged air temperatures measured above the pine canopy were recorded during August 2003 (29.4 °C), whereas the lowest was −9.3 °C, measured in January 2005. Summer vapour pressure deficit rose above 3 kPa during the summer of 2003, but very seldom reached 2 kPa in the summer of 2004 (Fig. 1). Total summer rainfall (June-August) was very low for 2003, compared to 2004 and 2005, and well below the long-term average for the same months (Tab. II). An unusually dry period occurred also between September 2004 and April 2005 during which rainfall was only 45% of the total precipitation during the same period in 2003–2004 (Tab. II).

Water content in the upper 30 cm of the soil was higher in the oak stand, with a range of 0.19–0.46 $cm^3\ cm^{-3}$, whereas in the pine stand it fell between 0.12 and 0.32 $cm^3\ cm^{-3}$. Rainy periods during autumn and spring lead to a recovery of soil water content after the summer of 2003, but this did not occur after the summer of 2004 (Fig. 1). The declining trend in soil moisture beginning in the autumn of 2004 was particularly appreciable in the oak stand, where it was also noticeable that soil moisture in the deeper soil layers (θ_{30-50}) was higher than superficial soil moisture during the summer in 2004, but not in 2005 (Fig. 1).

3.2. Water potentials

Predawn leaf water potentials were significantly higher in *Q. pubescens*, for both years 2004 (repeated measures ANOVA or ANOVAr, $P < 0.001$) and 2005 (ANOVAr, $P < 0.001$). Minimum values were ca. −0.8 and −0.9 MPa for oak and pine, respectively (Fig. 2a, 2b). On the contrary, midday ψ_l was significantly lower in *Q. pubescens* during 2004 (ANOVAr, $P = 0.002$) and 2005 (ANOVAr, $P < 0.001$). Minimum $\psi_{\mathrm{l,md}}$ (mean± SE) was much lower in *Q. pubescens* (−3.2 ± 0.11 MPa) than in *P. sylvestris* (−2.1 ± 0.06 MPa). The difference between $\psi_{\mathrm{l,pd}}$ and $\psi_{\mathrm{l,md}}$ was also significantly different between species for 2004 (ANOVAr, $P < 0.001$) and 2005 (ANOVAr, $P < 0.001$). Midday water potential decreased more steeply with decreasing $\psi_{\mathrm{l,pd}}$ in the oak plot (ANCOVA, $P < 0.001$, Fig. 3a), bringing about a greater increase in water potential difference with decreasing $\psi_{\mathrm{l,pd}}$ (Fig. 3b). The relationship between $\psi_{\mathrm{l,pd}}$ and θ_{0-30} (Fig. 3c) was different across plots (ANCOVA, $P < 0.001$). Water retention curves showed no difference between stands at high water potentials (Fig. 3d). However, at a value of $\psi_{5,0-30} = -1.5$ MPa, θ_{0-30} was 0.07 $cm^3\ cm^{-3}$ higher in the oak stand (Fig. 3d). These differences were related with a finer soil texture in the oak stand (Rubio, personal communication). We did not find a significant relationship between $\psi_{s,0-30}$ estimated from water retention curves and $\psi_{\mathrm{l,pd}}$, neither for Scots pine ($R^2 = 0.14$, $P = 0.115$), nor for pubescent oak ($R^2 = 0.22$, $P = 0.105$).

3.3. Sap flow and G_s responses to environmental variables

Maximum absolute values of midday sap flow rates were $3.6 \cdot 10^{-5}$ and $2.9 \cdot 10^{-5}$ kg m^{-2} leaf area s^{-1} for *P. sylvestris* and *Q. pubescens*, respectively. The dynamics of relative sap flow showed that its value measured at midday was higher in *Q. pubescens* when dry conditions occurred. This was the case during two exceptionally dry periods, one in the summer of the year 2003 and the other at the end of the unusual winter and spring drought of the year 2005 (Fig. 4). During the year 2004, though, the values and the dynamics were very similar in the two species. Sap flow relationships with D and R_n were similar for both species (Fig. 5). A marked decrease in relative sap flow with D above ca. 1.2 kPa was particularly appreciable during the year 2003 (Fig. 5a).

Scots pine relative sap flow also showed a declining trend with SMD_{0-30} in 2003 and 2005, but not in 2004 (Figs. 5c, 5f, 5i). Only during 2005 a clear decline in oak relative sap flow with SMD_{0-30} could be also observed (Fig. 5i). Relative sap flow declined linearly in both species with SMD, integrated for the whole soil profile examined (SMD_{0-60} in the pine plot and SMD_{0-50} in the oak plot), when this SMD was higher than 0.6 (*P. sylvestris*: $R^2 = 0.58$, $P = 0.004$; *Q. pubescens*: $R^2 = 0.51$, $P = 0.014$). Below this value, no apparent trend was observed. The rate of decline of relative sap flow did not differ between species, since we did not find significant differences between the slopes of the two linear regressions (ANCOVA, $P = 0.056$).

A more detailed examination of meteorological conditions and the response of $G_{\mathrm{s,md}}$ to the increased water deficits during the summer of 2003 showed that the ratio of sap flow-derived canopy stomatal conductance at midday between Scots pine and pubescent oak ($G_{\mathrm{s,md}}$ (pine)/$G_{\mathrm{s,md}}$ (oak)), declined with extreme D and SMD_{0-30} conditions, meaning that, under such circumstances, $G_{\mathrm{s,md}}$ in pine decreased proportionally more than in oak (Fig. 6). After substantial precipitation (> 40 mm), the subsequent refilling of soil water reserve caused pine $G_{\mathrm{s,md}}$ to increase more than oak $G_{\mathrm{s,md}}$, as revealed by the increase in the calculated ratio $G_{\mathrm{s,md}}$ (pine)/$G_{\mathrm{s,md}}$ (oak) (Fig. 6).

The values of $G_{\mathrm{s,md}}$ were higher for Scots pine, although beyond predawn water potentials of −0.8 MPa, Scots pine $G_{\mathrm{s,md}}$ was reduced to 10% of its maximum value (Fig. 7a)

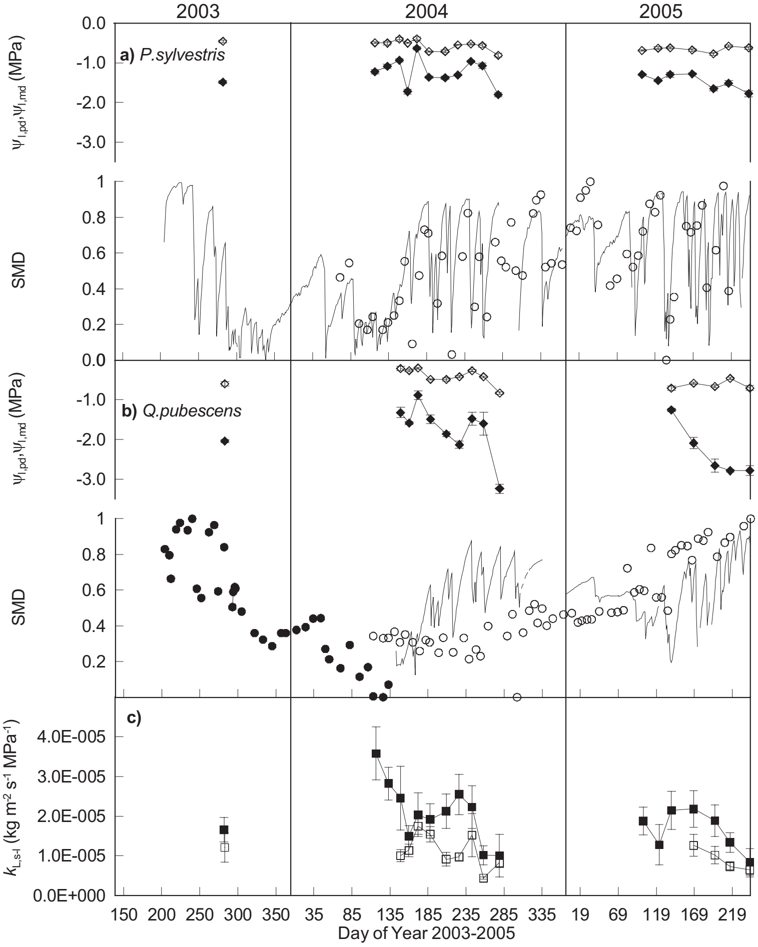

Figure 2. Seasonal evolution of predawn ($\psi_{l,\mathrm{pd}}$, open symbols) and midday ($\psi_{l,md}$, closed symbols) leaf water potentials in (a) *Pinus sylvestris* and (b) *Quercus pubescens*, together with soil moisture deficit (SMD) values estimated at the two depths where soil moisture was measured (0–30 cm and 30–50 cm (oaks), 30–60 cm (pines)). (c) Whole-plant hydraulic conductance ($k_{\mathrm{L,s-1}}$) expressed on a leaf area basis is also shown for *P. sylvestris* (closed squares) and *Q. pubescens* (open squares).

while pubescent oak kept $G_{\mathrm{s,md}}$ around 30% of its maximum within a range of $\psi_{l,pd}$ from −0.4 to −0.8 MPa (Fig. 7b).

3.4. Hydraulic conductance

Whole plant hydraulic conductance on a leaf area basis ($k_{\mathrm{L,s-1}}$) was ca. 1.2–2.6 times greater in *P. sylvestris* than in *Q. pubescens*, although the seasonal dynamics was similar for both species (Fig. 2c). Scots pine $k_{\mathrm{L,s-1}}$ decreased gradually from spring to summer in 2004. For 2005, however, springtime values were much lower than values for the same period in 2004. Pubescent oak $k_{\mathrm{L,s-1}}$ showed similar values across years. Scots pine $k_{\mathrm{L,s-1}}$ was negatively correlated with SMD_{0-30} ($R^2 = 0.46, N = 19, P = 0.002$), but we did not observe a significant relationship for pubescent oak ($R^2 = 0.24, N = 14, P = 0.080$). However, this lack of fit was driven by two data points, very close to the dates of leaf unfolding (DOY 149 and 160). Disregarding these data, a significant fit emerged ($R^2 = 0.57, N = 14, P = 0.002$).

3.5. Vulnerability to embolism and relationships between hydraulic conductance and gas exchange

The parameters (nonlinear regression estimate ±SE) of the vulnerability to embolism curve (Eq. (2), Fig. 8a) for *P. sylvestris* were $a = 1.17 \pm 0.13$ MPa^{-1} and $b = 2.78 \pm 0.11$ MPa (pressure causing a 50% loss of xylem conductivity). Maximum levels of wood-specific and leaf-specific hydraulic conductivities measured at the branch level were $K_W = 4.4 \cdot 10^{-4} \pm 0.74 \cdot 10^{-4}$ m^2 wood area MPa^{-1} s^{-1} and $K_{\mathrm{L}} = 2.7 \cdot 10^{-7} \pm 0.27 \cdot 10^{-7}$ m^2 projected leaf area MPa^{-1} s^{-1}, respectively. Combining the measured leaf water potentials (Fig. 2a) and the information from the vulnerability curves (Fig. 8a), we observed that the maximum predicted PLC in the field approached 30%. Contrastingly, according to the vulnerability curve by [9], pressure causing a 50% loss of xylem conductivity in *Q. pubescens* was ca. −3.4 MPa (Fig. 8b).

P. sylvestris showed reductions of $G_{\mathrm{s,md}}$ to less than 10% of its maximum value when leaf water potentials fell beyond −2.0 MPa, meaning a 30% of xylem conductivity losses

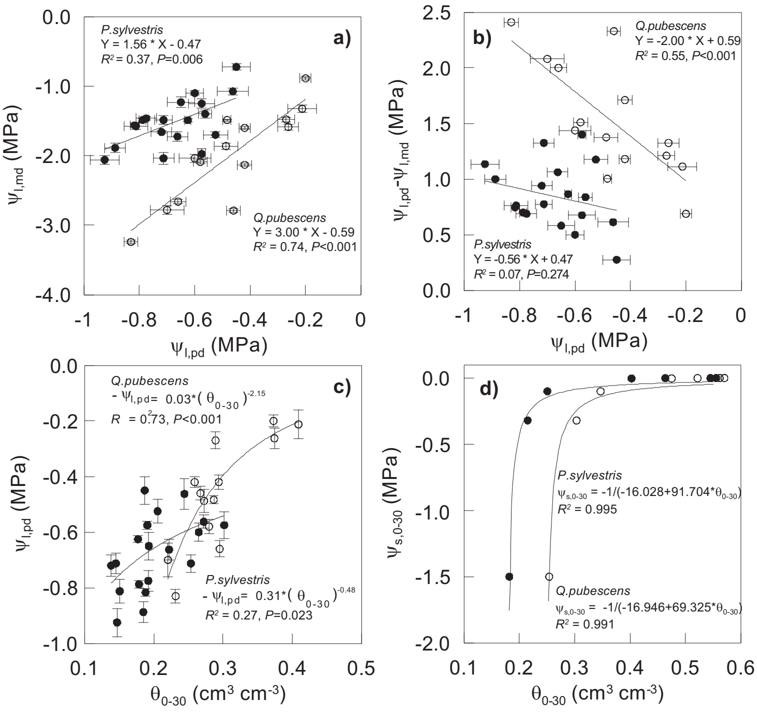

Figure 3. Relationships between (a) predawn ($\psi_{l,pd}$) and midday ($\psi_{l,md}$) leaf water potentials, (b) between water potential difference ($\psi_{l,pd} - \psi_{l,md}$) and predawn water potential, and (c) between $\psi_{l,pd}$ and soil moisture in the upper 30 cm (θ_{0-30}). Water retention curves, showing relationships between soil water potential ($\psi_{s,0-30}$) and θ_{0-30}, are also shown (d). Closed symbols represent data points for *P. sylvestris* and open symbols, for *Q. pubescens*.

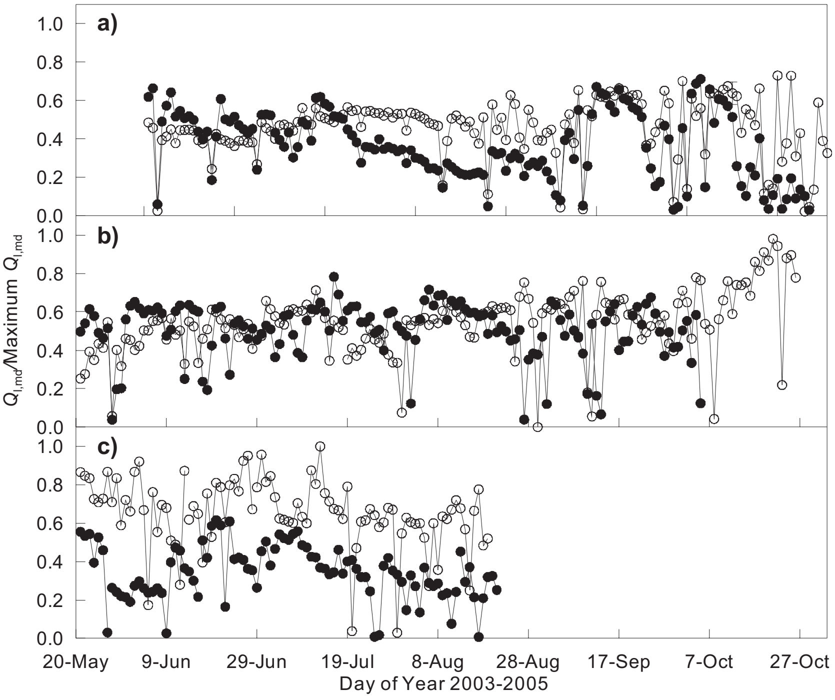

Figure 4. Sap flow per unit leaf area relative to its maximum value for *P. sylvestris* (closed symbols) and *Q. pubescens* (open symbols) during (a) 2003, (b) 2004 and (c) 2005.

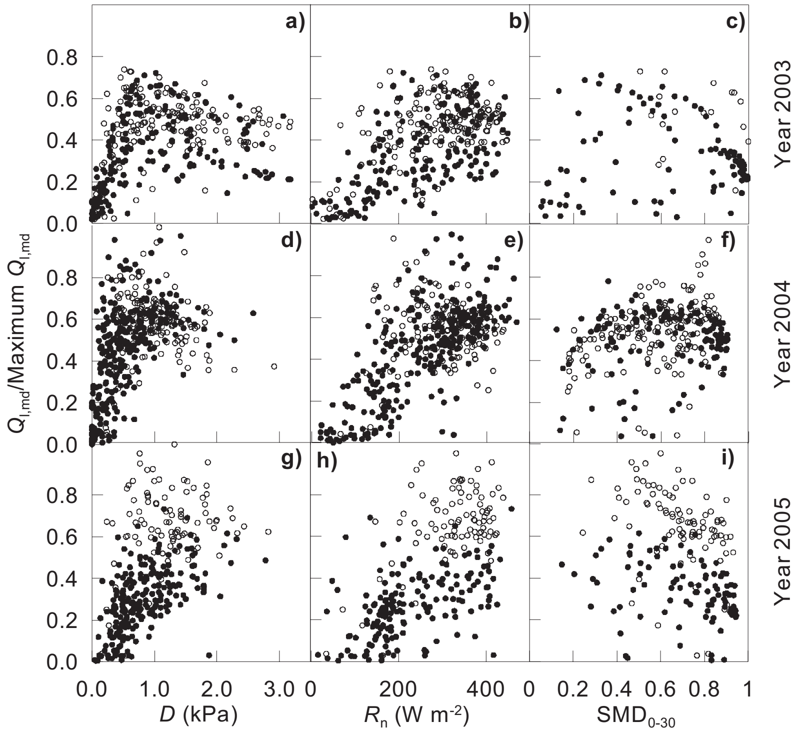

Figure 5. Relationships between relative sap flow and environmental variables for the three years of study for *Pinus sylvestris* (closed symbols) and *Quercus pubescens* (open symbols). Panels (a), (d) and (g) show relationships with vapour pressure deficit (D); (b), (e) and (h), with net radiation (R_n) and (c), (f) and (i) with superficial soil moisture deficit (SMD_{0-30}).

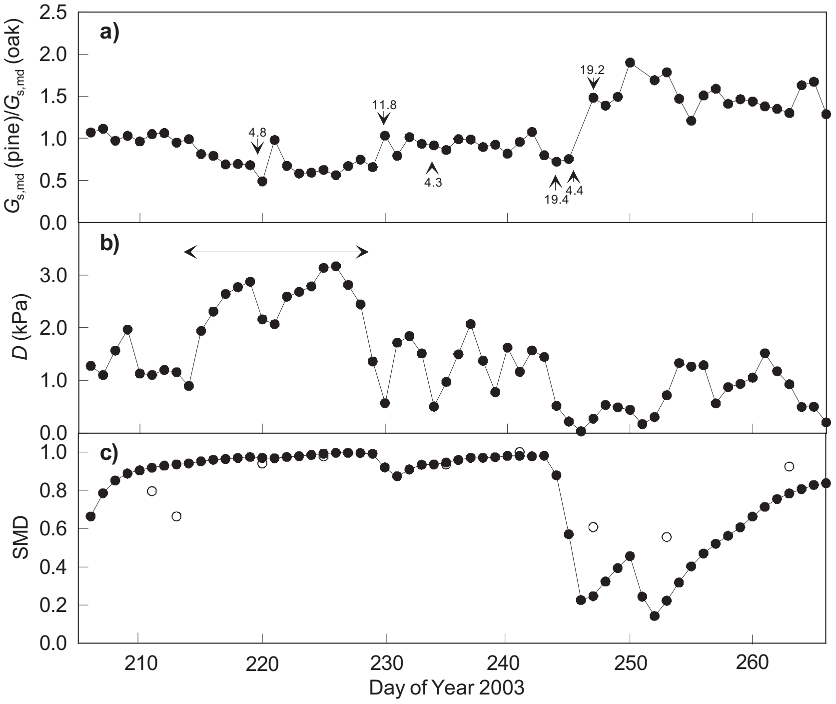

Figure 6. (a) Ratio between pine and oak midday canopy stomatal conductances ($G_{s,md}$) during the dry episode of the summer of 2003 and posterior recovery. Arrow heads and numbers show rainfall amounts. (b) Corresponding conditions of daytime-averaged vapour pressure deficit (D). The period with extreme D conditions is marked with an horizontal arrow. (c) Soil moisture deficit in the upper soil layer (SMD_{0-30}), continuously measured in the pine plot (closed symbols) and fortnightly in the oak plot (open symbols).

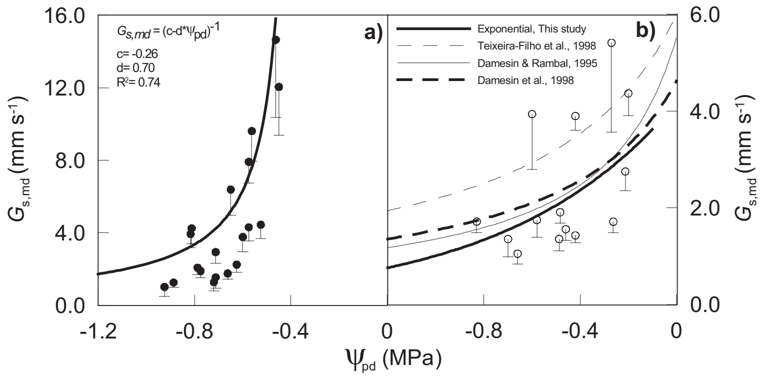

Figure 7. Midday canopy stomatal conductances ($G_{\mathrm{s,md}}$) for (a) *Pinus sylvestris* and (b) *Quercus pubescens* related to the value of predawn leaf water potential. The fitted functions are based on Acherar and Rambal (1992), except for the exponential fit used for *Q. pubescens* data in the present study.

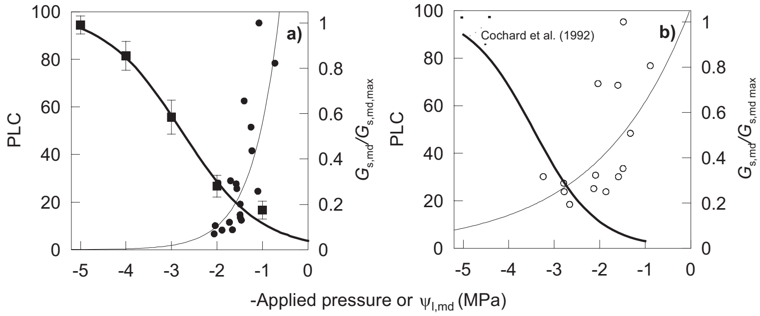

Figure 8. (a) Percent loss of hydraulic conductivity (PLC) for *Pinus sylvestris* branches with respect to the negative of applied pressure (MPa). The curve was fitted to all the individual measurements of PLC but closed squares are the average of PLC's calculated for $n = 10$ branches. The variation of the ratio between midday canopy stomatal conductance ($G_{\mathrm{s,md}}$) and its maximum value ($G_{\mathrm{s,md,max}}$), and midday leaf water potential ($\psi_{\mathrm{l,md}}$) is also shown for *P. sylvestris* (a) and for *Q. pubescens* (b). For the latter we plotted the vulnerability curve obtained by Cochard et al. (1992) for the same species.

(Fig. 8a). At the same water potentials, *Q. pubescens* still maintained $G_{\mathrm{s,md}}$ at 40% of its maximum value with a corresponding PLC of less than 10%, according to [9] (Fig. 8b).

Finally, daily maximum values of leaf-level stomatal conductance (g_{s}) were closely linked to $k_{\mathrm{L,(s-l)}}$ in both species, following a power relationship for Scots pine and a logarithmic one for pubescent oak (Fig. 9). In addition, a significant relationship was also established between Scots pine PLC predicted by the vulnerability curves and maximum g_{s} (data not shown).

4. DISCUSSION

4.1. Meteorology, soil moisture and water potentials

Under similar meteorological conditions, soil moisture in the oak stand was higher than in the pine stand throughout the period of study. Comparisons between long-term soil moisture measurements between the same oak stand and other Scots pine stands in the area show identical results [39]. These differences may be attributed to the different interception characteristics of pine and oak canopies, the role of litterfall preventing direct evaporation from the soil in the deciduous stand, differences in the transpiration component of stand water balance (understorey and overstorey) and intrinsic differences in soil hydraulic properties.

Predawn water potentials were unrelated to estimated soil water potentials in the upper 30 cm of the soil. As $\psi_{\mathrm{l,pd}}$ is considered to represent the water potential of the wettest soil layer 'sensed' by the roots [5], our results suggest that trees are exploiting deeper water resources. Indeed, the higher $\psi_{\mathrm{l,pd}}$ in *Q. pubescens* could indicate a more efficient strategy in exploiting soil water resources, especially in depth [45]. We did not find a good correspondence between $\psi_{\mathrm{l,pd}}$ and $\psi_{\mathrm{s,0-30}}$ in either species, indicating that ψ_{s} estimated for the upper 30 cm was not representative of the whole rooting depth.

Under identical meteorological conditions, more negative leaf water potentials occur in pubescent oak, while for Scots pine, leaf water potentials hardly fall below −2 MPa. While much lower leaf water potentials (ca. −4.5 MPa) have been recorded for pubescent oak throughout the Mediterranean region [14, 43], the values found for Scots pine are among the lowest ever measured, with the exception of even drier populations in NE Spain [28].

The difference between $\psi_{\mathrm{l,pd}}$ and $\psi_{\mathrm{l,md}}$ increased with decreasing $\psi_{\mathrm{l,pd}}$ for pubescent oak, therefore allowing a greater increase in the driving force for transpiration as edaphic drought developed. This pattern was not observed in

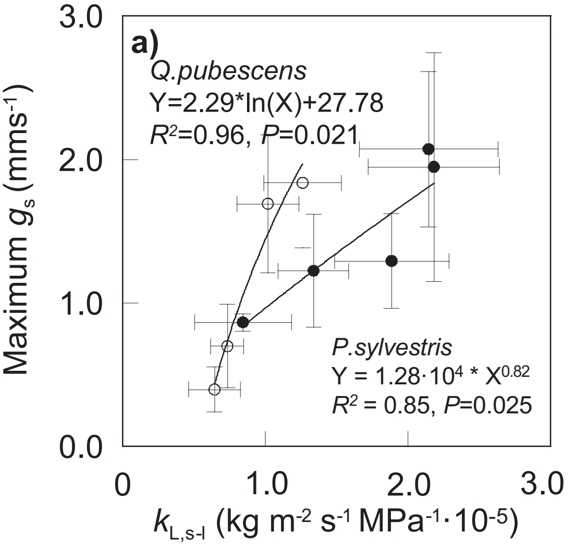

Figure 9. Relationship between maximum stomatal conductance to water vapor measured at the leaf-level (g_s) and whole-plant hydraulic conductance ($k_{\mathrm{L,s-l}}$). (Closed symbols represent *P. sylvestris* and open symbols, *Q. pubescens*).

P. sylvestris, a first indication of an enhanced stomatal control by this species.

4.2. Sap flow and G_s responses to environmental variables and predawn leaf water potential

We observed that pubescent oak maintained higher sap flow rates during periods with lower soil water availability, such as the summer of 2003 and the year 2005. When soil moisture was not limiting (year 2004), both species showed similar values of relative sap flow but when dry periods occurred (in 2003 and 2005), the enhanced sensitivity of Scots pine sap flow to superficial SMD was clear. We also observed strong responses of relative sap flow in both species to integrated SMD over the soil profile when SMD was larger than 0.6.

High *D*'s and soil moisture deficits made G_s decrease proportionally more in pine than in oak. These findings are in agreement with the general responses of both species to water deficits observed elsewhere. Pubescent oak maintains high transpiration rates despite showing very low leaf water potentials [14, 32], even lower than the turgor loss point [27], while Scots pine efficiently closes stomata beyond a threshold in soil moisture [22] and in response to high vapour pressure deficits [41] .

Scots pine $G_{\mathrm{s,md}}$, was reduced to 10% of its maximum value when $\psi_{\mathrm{l,pd}}$ values approached −0.8 MPa. Perks et al. observed that the ratio between canopy conductance of droughted and control Scots pine trees fell to 0.2 when minimum $\psi_{\mathrm{l,pd}}$ of −0.8 MPa were reached [35]. Also Sturm et al. [41] showed similar reductions of leaf-level stomatal conductance with decreasing $\psi_{\mathrm{l,pd}}$. However, at the lowest measured $\psi_{\mathrm{l,pd}}$, pubescent oak kept stomatal conductance at higher levels, about 30% of the maximum value. The relationship between pubescent oak $G_{\mathrm{s,md}}$ and $\psi_{\mathrm{l,pd}}$ was similar to others found for the same species [14]. Despite that the absolute values of conductance were higher in another location in Portugal [42], the reduction with $\psi_{\mathrm{l,pd}}$ was also similar to the values that we report.

4.3. Hydraulic conductance

Whole-plant hydraulic conductance calculated on a half-total leaf area basis was higher in Scots pine than in pubescent oak. The values of *P. sylvestris* $k_{\mathrm{L,s-l}}$ were within the range reported in the literature [3]. The range of *Q. pubescens* $k_{\mathrm{L,s-l}}$ observed in this study is inferior to published results obtained for saplings of the same species, with $k_{\mathrm{L,s-l}}$ between 4.5 and $6.5 \cdot 10^{-5}$ kg m^{-2} s^{-1} MPa^{-1} [27, 32]. Values of $k_{\mathrm{L,s-l}}$ measured in fully-grown *Quercus petraea* trees from another montane area of the Iberian Peninsula also ranged between 4.0 and $7.0 \cdot 10^{-5}$ kg m^{-2} s^{-1} MPa^{-1} [2].

Although Scots pine possesses the highest branch-level conductivities among the Pinaceae, typical sapwood conductivities of pines are lower than those of deciduous oak species [7, 29]. Published branch-level measurements of K_s in pubescent oak [44] are almost an order of magnitude higher than those found for Scots pine's maximum wood-related conductivity (K_W) in this study. However, Scots pine has a lower $A_L : A_S$, achieving a higher hydraulic sufficiency than pubescent oak. This compensation mechanism was proposed by Becker et al. [3] to explain the similar hydraulic sufficiency observed between conifers and angiosperms.

We have found that $k_{\mathrm{L,s-l}}$ was negatively correlated with soil moisture for both species. Accordingly, high levels of $k_{\mathrm{L,s-l}}$ in Scots pine were only reached during the spring of 2004, before soil moisture deficits developed. Further decreases in $k_{\mathrm{L,s-l}}$ were observed as the summer progressed in 2005. Our results agree with those of Irvine et al. [22] who found that hydraulic resistance increased significantly for trees under a drought treatment but was maintained essentially constant for control trees.

The decline in $k_{\mathrm{L,s-l}}$ was clear during 2005 for pubescent oak, in parallel with the increase in superficial and deep SMD. Other authors have reported that, during the summer, whole-plant hydraulic conductance declined up to 50% of its maximum value in the deciduous *Quercus petraea* [2]. Consistent with these observations, a maximum of 40% loss of conductivity at the branch-level has been reported for pubescent oak during mild or slightly dry years [27, 32]. Nevertheless, maximum conductivity losses of *ca.* 70% were observed under severe water stress (minimum $\psi_{\mathrm{l,pd}}$ of −3.6 MPa) [43].

4.4. Stomatal control and xylem embolism: coordination of liquid-phase and vapour phase conductances

The studied Scots pine population was slightly more vulnerable to drought-induced embolism than other populations from drier montane areas of the NE Iberian Peninsula [28], but was more resistant than individuals from Central Europe [11].

We found a rapid decline in the fraction of maximum stomatal conductance before significant losses of conductivity occurred in the stem xylem according to the measured vulnerability curve. Irvine et al. [22] also found increases in hydraulic resistance without significant xylem embolisms in the trunk, suggesting an increase in below-ground resistances with drought development. To illustrate the Scots pine's tight stomatal control over xylem embolism, we calculated the safety margin between the water potential causing 10% loss of conductivity and the water potential reducing stomatal conductance to a 10% of its maximum. This value was ca. 1.1 MPa, and places Scots pine among the species with strong stomatal control of embolism [6].

Pubescent oak was more resistant to xylem embolism and therefore maintained a higher stomatal opening, with less xylem conductivity losses than Scots pine at a given water potential (Fig. 8). The corresponding safety margin for *Q. pubescens* would be ca. 3.8 MPa. This strategy of keeping large safety margins has been reported for species experiencing seasonal drought episodes [6], in line with the Mediterranean origin of this species. However, these conclusions are drawn from a vulnerability curve which has not been determined in the population we studied, and must be held with caution. A high variability in hydraulic traits among closely-related Submediterranean deciduous oaks has been recently reported in two studies carried out in the Iberian Peninsula [12, 19]

Finally, we also found a significant correlation between $k_{\mathrm{L,s-l}}$ and independent measurements of maximum leaf-level g_{s} in both species (Fig. 9) as observed elsewhere for pine [1] and some angiosperm species [33], but still unreported for oaks. A linear relationship between g_{s} and $k_{\mathrm{L,s-L}}$ has been suggested to be characteristic of isohydric species (regulate ψ_{l} at a constant value), while a curvilinear relationship has been attributed to anisohydric species (intermediate between constant ψ_{l} regulation and no ψ_{l} regulation) [20]. The shape of the relationships between $g_{\mathrm{s,max}}$ and $k_{\mathrm{L,s-L}}$ would imply isohydric and anisohydric behaviour for pine and oak, respectively, as could be also inferred from the seasonal course of leaf water potentials (Fig. 1a, 1b).

4.5. Implications of the observed responses to water deficits

Information about the response to water deficits of co-occurring Scots pine and pubescent oak is scarce. Nevertheless, in one recent study both species showed only a slightly higher influence of water deficits in Scots pine, with the largest differences found for dry periods [49]. In general, other studies involving coexisting pine and oak species show that the latter has a more negative threshold ψ_{l} for stomatal closure and a higher ψ_{pd}, meaning greater avoidance of soil water stress [24].

The fact that two contrasting species are able to coexist suggests a significant functional convergence in plant responses to the environment [30]. Nevertheless, extreme drought conditions will definitely affect more negatively the least resistant species. In fact, Scots pine populations in the study area showed premature leaf loss during August 2003 and drought-induced mortality occurred locally in other populations growing at lower elevations at the end of the spring of the year 2005 (personal observation). Besides, drought-induced mortality has been repeatedly observed in Scots pine stand from Mediterranean [28] and Central Europe populations [4]. On the contrary, *Q. petraea* was less affected than other coexisting species by the extreme 2003 summer drought in Central Europe [26].

The distribution of both species in NE Spain support the view that pubescent oak is more adapted to drought, as it can be found from pre-litoral to montane areas, while Scots pine is restricted to the latter. The increased incidence of extreme drought periods in the future [21] is likely to affect Scots pine more severely than pubescent oak, which can bring about significant changes in the composition of Mediterranean montane forests.

5. CONCLUSIONS

The overall response to water deficits of the studied Scots pine and pubescent oak under equivalent climatic conditions was similar, but differences appeared when extreme soil moisture deficits and high evaporative demand conditions occur. Pubescent oak showed higher predawn leaf water potentials, which is indicative of a better access to soil moisture. Scots pine showed midday leaf water potentials which were intermediate between those measured in more humid and cooler locations and those observed in drier locations in NE Iberian Peninsula, but generally less negative than the values found for oak. Although both species showed decreasing sap flow beyond a threshold vapour pessure deficit, pubescent oak maintained higher relative sap flow during the intense drought in 2003, and showed less stomatal closure than Scots pine during that period. Midday canopy-averaged stomatal conductance declined in both species with decreasing midday leaf water potentials, but pubescent oak maintained a higher fraction of maximum conductance at the minimum water potentials. Both species showed coordination between leaf-level gas exchange and hydraulic conductance, but. Scots pine showed a tighter stomatal control to avoid substantial hydraulic conductivity losses. Published data on vulnerability to embolism in pubescent oak revealed that it was comparatively more resistant to xylem embolism. We can therefore expect that pubescent oak will be less affected than Scots pine by the predicted increase in aridity in the Mediterranean region.

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