



**Measuring and modelling transpiration
of pine and oak forest stands
in a Mediterranean mountain area (Vallcebre, NE Spain)**

TESI DOCTORAL

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5. Response of co-occurring Scots pine (*Pinus sylvestris* L.) and pubescent oak (*Quercus pubescens* Willd.) to soil and atmospheric water deficits.

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Writing is the single activity in India that doesn't pay, and anyway this man wrote about the poor: no one was interested in reading about poor people. He knew, because the poor were his business.

'Famine relief, resettlement, drought prevention, underprivileged, anything you can name. It is a headache sometimes. But my books don't sell, so I have no choice. You could call me an organizer'

'How do you prevent droughts?'

'We have programmes'

I saw committees, position papers, conferences –and dusty fields.

'Have you prevented any lately?'

'We are making steady progress', he said. 'But I would rather write novels'

The great railway bazaar, Paul Theroux

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Abstract

The physiological responses to water deficits of Scots pine (*Pinus sylvestris* L.) and pubescent oak (*Quercus pubescens* Willd.) under similar climatic conditions has been studied in two stands located in the Eastern Pyrenees between the years 2003 and 2005. In these plots, we carried long-term measurements of leaf water potentials and sap flow, together with meteorological and soil moisture conditions. Leaf level gas exchange in both species was measured in 2005 and additionally, vulnerability to embolism was also assessed for Scots pine. Leaf water potentials measured at predawn were generally higher for oak, which could be the result of the finer soil texture in the oak stand or reflect differences in rooting behaviour between species. Leaf water potentials at midday were generally lower for pubescent oak, with minimum values of -3.2 MPa for this species and -2.1 MPa measured in Scots pine. Sap flow relative to its species-specific maximum value was shown to decline with increasing D above a threshold of ca. 1.2 kPa for both species. Nevertheless, extreme conditions of evaporative demand and soil moisture deficit (SMD) measured during the summer of 2003, promoted an enhanced stomatal control in Scots pine. Pubescent oak also maintained a higher fraction of maximum conductance at the minimum water potentials. The seasonal course of hydraulic conductance on a leaf area basis ($k_{L,S-I}$) showed a considerable decrease from spring to summer for Scots pine. Pubescent oak $k_{L,S-I}$ was an order of magnitude lower than that of pine, and showed similar decreases as pine during the summer of the year 2005. Scots pine closed stomata to prevent substantial stem xylem embolism, but the comparison between observed stomatal regulation and published vulnerability curves for pubescent oak, was not concluding. Both species show combinations of structural and functional features that allow them to coexist in Mediterranean montane environments. Nevertheless, the results of this study and the existing evidence suggest that pubescent oak is more resistant to extreme drought conditions.

Resum

La resposta fisiològica al dèficit hídric del pi roig (*Pinus sylvestris* L.) i del roure martinenc (*Quercus pubescens* Willd.) en les mateixes condicions climàtiques, ha estat estudiada en dos coberts situats al Pre-Pirineu Oriental durant els anys 2003-2005. En aquestes parcel·les, es realitzaren mesures de potencials hídrics a les fulles i flux de saba, a més de registrar-se les variables meteorològiques i la humitat del sòl. Adicionalment, es mesurà l'intercanvi gasós a nivell de fulla en ambdues espècies durant el 2005, i la vulnerabilitat a l'embolisme del pi roig. Els potencials hídrics mesurats a l'alba (*predawn*) foren generalment majors pels roures, podent ser conseqüència d'una textura del sòl més fina en la parcel·la de roures o reflex de diferències en el comportament de les arrels en les dues espècies. Els potencials hídrics a migdia foren generalment menors en els roures, amb valors mínims de -3.2 MPa per aquesta espècie i de -2.1 MPa pel pi roig. El flux de saba relatiu al màxim específic de cada espècie disminuï a l'augmentar el dèficit de pressió de vapor (D) per sobre d'un llindar d'aproximadament 1.2 kPa per ambdues espècies. No obstant, les condicions extremes de demanda evaporativa i de dèficit d'humitat del sòl (SMD) mesurades durant l'estiu del 2003, van accentuar el control estomàtic del pi roig. El roure martinenc va mantenir una major fracció de la màxima conductància a potencials hídrics mínims. L'evolució estacional de la conductància hidràulica en base a l'àrea foliar ($k_{L,S-I}$) mostrà una disminució considerable entre la primavera i l'estiu pel pi roig. La $k_{L,S-I}$ en els roures martinencs fou un ordre de magnitud inferior que en els pins, i mostrà una disminució simular a la dels pins durant l'estiu del 2005. Els resultats demostren que el pi roig tanca els estomes per prevenir l'embolisme del xilema, en canvi en el roure, la comparació de la regulació estomàtica observada i les corbes de vulnerabilitat publicades per aquesta espècie no han permès obtenir conclusions clares. Ambdues espècies mostren combinacions dels trets estructurals i funcionals que els permeten coexistir en ambients de muntanya Mediterrània. De tota manera, els resultats d'aquest estudi, entre d'altres evidències, suggereixen que el roure martinenc és més resistent a les condicions d'eixut sever.

Introduction

Scots pine (*Pinus sylvestris* L.) and pubescent oak (*Quercus pubescens* Willd.) are two of the most representative tree species in montane areas of NE Spain. While Scots pine is a Eurosiberian species with a broad distribution, pubescent oak, restricted to southern Europe (Jalas et al., 1999), is considered a submediterranean species (Ceballos and Ruiz de la Torre 1979). In the Iberian Peninsula, pubescent oak occurrence coincides with the transition zone between Mediterranean-type and more humid environments (Blanco et al. 1997). In these Mediterranean montane areas, where the two species co-occur, they undergo a wide range of environmental conditions, from persistent sub-zero temperatures during winter to occasionally intense dry summer periods.

Although both species share the same habitat, they are completely different in the main morphological traits of the water transport pathway from roots to leaves. Scots pine is an evergreen needleleaved conifer, with tracheid-bearing xylem and pubescent oak is a winter deciduous or marcescent broadleaved species, with vessel-bearing xylem and deep root systems. Despite its relatively low sapwood conductivity as a conifer (Pallardy et al. 1995), Scots pine shows very low leaf-to-sapwood area ratios ($A_L:A_S$) (DeLucia et al. 2000; Mencuccini and Bonosi 2001), while the contrary usually holds for deciduous oak species, which show higher efficiency of the conducting elements and higher $A_L:A_S$. (Villar-Salvador et al. 1997). This combination of traits results in similar hydraulic sufficiency at the whole-plant level (Becker et al. 1999).

With regard to water economy strategies, Scots pine closes stomata when soil moisture deficit has reached a specific threshold (Irvine et al. 1998) whereas pubescent oak maintains high transpiration rates despite the incidence of drought (Nardini and Pitt 1999), partly due to the ability to extract water from deep soil layers and groundwater (Valentini et al. 1992). These differences in stomatal control might be related to different vulnerability to embolism of the two species. While Scots pine is relatively vulnerable to embolism, and accordingly shows a tight stomatal control (Irvine et al. 1998), vulnerability curves of *Q. pubescens* show contradictory results (Cochard et al. 1992a; Tognetti et al. 1998). Nevertheless, although the avoidance of substantial embolism has been claimed for European oak species (Cochard et al. 1996), pubescent oak's high transpiration rates under drought conditions points at a less strict stomatal regulation in this species.

Trees accommodate their transpiration rates to the capacity of the hydraulic system of supplying the canopy leaves with water by means of a close coordination between hydraulic and stomatal conductance (Meinzer 2002). This relationship often results in the convergence of plant function across co-existing species, in a manner that, the combination of different morphological or anatomical features, may yield similar

responses to environmental conditions (Meinzer 2003). Recent studies on co-occurring Scots pine and pubescent oak have shown only slightly higher water deficits in the former species (Zweifel et al. 2005). However, there is increasing evidence that extreme drought episodes affect Scots pine particularly (Martínez-Vilalta and Piñol 2002), while deciduous oaks as for example *Quercus petraea*, even less drought-adapted than pubescent oak, have been shown to tolerate such conditions (Leuzinger et al. 2005).

In this study we compare the physiological behaviour of these two species under the Mediterranean montane conditions of the Eastern Pyrenees. Scots pine has increased its extension due to its colonizing capacity and the anthropic influence (Poyatos et al. 2003), dominating the landscape in these areas, while the climatic pubescent oak has seen its extension strongly reduced over the years. Particularly, the aims of our study are: (1) to find whether there are significant differences between species in the sensitivity of sap flow to varying conditions of soil moisture and evaporative demand, (2) to investigate the variations in water potential and hydraulic conductance and (3) to relate such variations in hydraulic conductance with stomatal control of transpiration, specially for *P.sylvestris*, given its dominance and relevance in Mediterranean mountain landscapes.

Material and methods

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). 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. Mudstone and sandstone are the principal underlying lithologies, originating sandy-loam soils about 65 cm deep (Rubio, pers. com.). The oak plot is located just 0.8 km apart from the pine plot and it is characterised by the presence of other woody species such as *Prunus avium* L., *Fraxinus excelsior* L. and a dense understorey, mainly composed of *Acer campestre* L., *Buxus sempervirens* L., *Prunus spinosa* L., *Rubus spp.* and *Rosa spp.* The upper soil, which is formed by a loamy matrix and limestone boulders, is about 50 cm deep (Rubio 2005). Stand structure differs in both plots in terms of stem density and understorey cover, but they have very similar leaf area indices (Chapter 2, Table 1).

Monitoring design

Above-canopy meteorology, soil moisture and sap flow were measured continuously between May 2003 and August 2005. For details of meteorological and soil moisture instrumentation see Chapters 2 and 3.

Sap flow

In each plot, sap flow was measured with heat dissipation probes (see Chapters 2 and 3) in a maximum of 12 trees simultaneously (Table 1). Sap flow gauges were installed at

Table 1. Tree sizes and period when sap flow was measured in each tree (heat dissipation monitoring and heat field deformation radial patterns measurements).

| | Tree ID | DBH (cm) | Period of HD sap flow measurements | Period of radial patterns measurements |
|---------------------|---------|----------|------------------------------------|--|
| <i>P.sylvestris</i> | 1 | 6.65 | May 2004-Aug 2005 | |
| | 2 | 10.15 | Jun 2003-Aug 2005 | |
| | 3 | 11.25 | May 2004-Aug2005 | |
| | 4 | 12.65 | May 2004-Aug 2005 | 217-220 (5-8 Aug) |
| | 5 | 13.30 | May 2004-Aug2005 | |
| | 6 | 15.90 | Jun2003-Aug 2005 | 203-216 (22 Jul-4 Aug) |
| | 7 | 17.95 | May 2004-Aug 2005 | 196-203 (15-22 Jul) |
| | 8 | 19.40 | Jun 2003-Mar 2004 | |
| | 9 | 19.85 | Jun 2003-Aug 2005 | |
| | 10 | 20.35 | Jun 2003-Aug 2005 | 102-110 (2-10 Apr) |
| | 11 | 22.50 | May 2004-Aug 2005 | 181-186 (30 Jun-5 Jul) |
| | 12 | 27.85 | Jun 2003-Aug 2005 | 116-120 (26-30 Apr) |
| | 13 | 29.3 | May 2004-Aug2005 | 173-181 (22-30 Jun) |
| <i>Q.pubescens</i> | 1 | 8.7 | May 2003-Oct 2004 | |
| | 2 | 12.6 | May 2003-Sept 2004 | |
| | 3 | 14.5 | May 2003-Aug 2004 | |
| | 4 | 17.85 | May 2003-Aug 2005 | |
| | 5 | 19.2 | May 2003-Nov 2004 | |
| | 6 | 20.9 | May 2003-Aug 2005 | |
| | 7 | 21.1 | May 2003-Aug 2005 | |
| | 8 | 21.5 | May 2003-Oct 2004 | |
| | 9 | 26.2 | May 2003-Aug 2005 | |
| | 10 | 26.7 | May 2003-Sept 2004 | |
| | 11 | 34.5 | May 2003-Sept 2004 | |
| | 12 | 38.2 | May 2003-Sept 2004 | See Chapter 3 for pubescent oak |

breast height, and covered with reflective insulation to avoid the influence of natural temperature gradients in the trunk. 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 (Clearwater et al. 1999).

Sap flow measured in Scots pine by Granier sensors was corrected for radial variability in sap flow density as done previously for pubescent oak (see Chapter 3). Briefly, a multi-point Heat Field Deformation sap flow sensor (Nadezhdina et al. 1998) 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, 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 (see Chapter 3 for details and results for pubescent oak). 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 with respect to its maximum value (see for example Leuzinger et al., (2005)) and then analysed how it varied according to vapour pressure deficit (D), net radiation (R_n) and soil moisture deficit SMD (see for example, Chapter 2 for details on calculation of SMD).

We also calculated canopy stomatal conductance at midday ($G_{s,md}$) derived from sap flow measurements (Whitehead and Jarvis 1981), averaging the individual tree values of canopy stomatal conductance (G_s) at the 15-min scale from 11:00 to 13:00 solar time.

Leaf-level gas exchange

Leaf stomatal conductance to CO_2 was measured in both species with a portable gas exchange system (LiCor 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. Conductances to CO_2 were converted to conductances to water vapour ($g_{s,wv}$) multiplying by a factor of 1.6, which corresponds to the ratio between water vapour and CO_2 diffusivities.

Leaf water potential measurements

Pre-dawn (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).

Vulnerability to embolism in P.sylvestris branches

Additionally, given the quantitative importance of Scots pine in the study area, vulnerability to embolism was assessed only for this species. A total of 10 mid-crown branches were sampled at the end of July 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-Cor 3100, LiCor Inc., NE, USA). Vulnerability to embolism was measured using the air injection method (Cochard et al. 1992b). 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 chamber with both ends protruding. The proximal end was connected to a tubing system filled with a filtered ($\Phi=0.22\ \mu\text{m}$) and degassed solution of HCl (pH around 2). This solution was injected at a pressure of *ca.* 0.75 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 preweighed 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 minutes 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 (Pammenter and Vander Willigen 1998), fitted using nonlinear least squares regression (procedure nls in R Statistical Software, v.2.0.1).

$$PLC = 100 / (1 + \exp(a(\psi - b))) \quad (1)$$

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

Hydraulic conductance

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

$$k_{L,(s-l)} = \frac{Q_{L,md}}{\psi_s - \psi_l - \rho gh} \quad (2)$$

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}) h is mean height of the trees (m). The use of midday sap flow rates has been recommended to minimize the effects of time lags between transpiration and sap flow (Irvine et al. 2004).

Table 2. Rainfall during the selected periods compared to the long-term average.

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

* Of the previous year

† Latron et al., in press

Results

Meteorology and soil moisture during the study period

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. In general, the pine stand was only slightly wetter and cooler than the oak stand. Conditions of evaporative demand varied greatly across years. Summer vapour pressure deficit rised above 3 kPa during the summer of 2003, but very seldom reached 2 kPa in the summer of 2004 (Fig. 1). Rainfall amounts for the summer period (June-August) were very low for 2003, compared to 2004 and 2005, and well below the long-term average for the same months (Table 2). An unusually dry period occurred between September 2004 and April 2005 during which rainfall was only 45% of the total precipitation during the same period in 2003-2004 (Table 2).

Water content in the upper 30 cm of the soil was in broad terms higher in the oak stand, with minimum and maximum values of $0.19 \text{ cm}^3 \text{ cm}^{-3}$ and $0.46 \text{ cm}^3 \text{ cm}^{-3}$, whereas the range in the pine stand was $0.12\text{-}0.32 \text{ cm}^3 \text{ cm}^{-3}$. Rainy periods during autumn and spring lead to a recovery of θ_{0-30} 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).

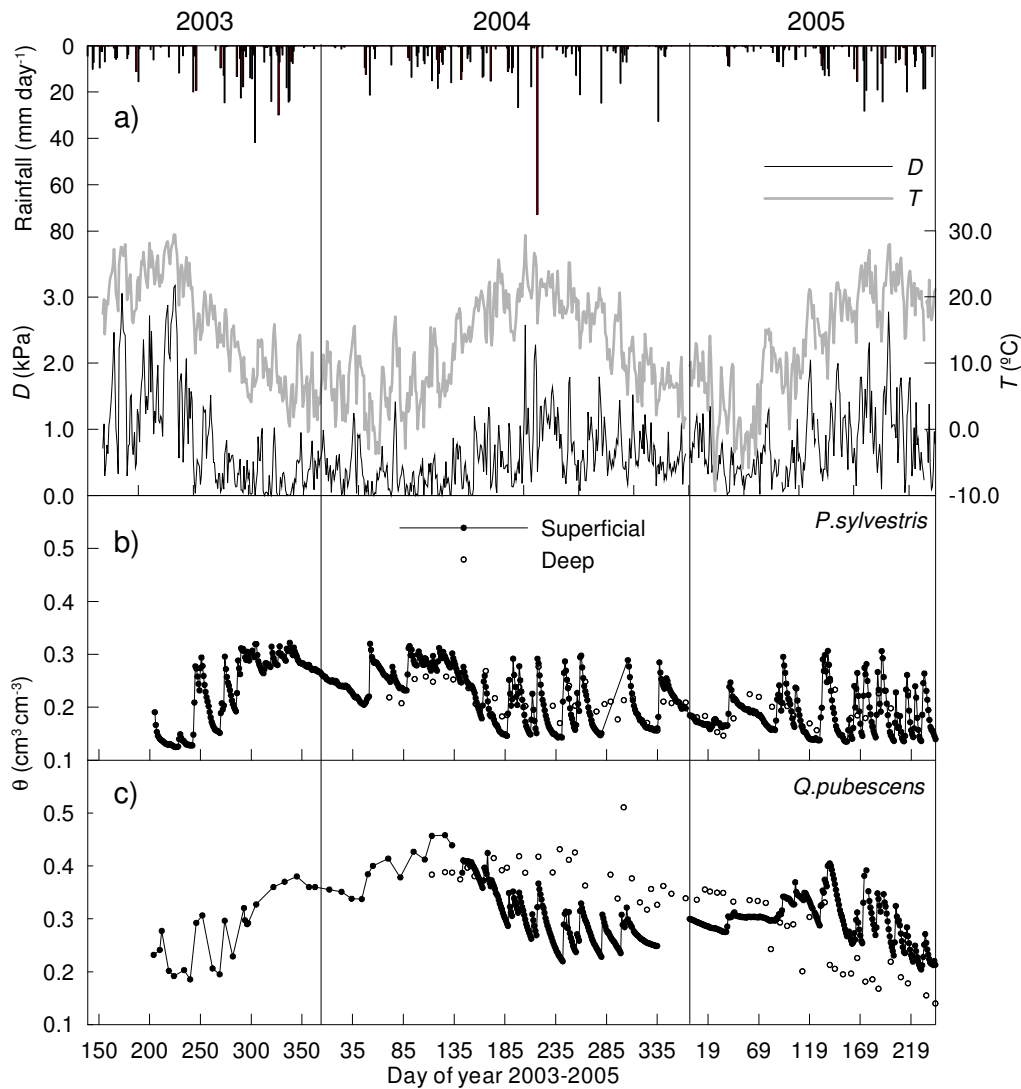


Figure 1. Meteorology and soil moisture during the whole period of study (June 2003-August 2005). Air temperature (T) and vapour pressure deficit (D) only shown for the pine plot, and rainfall measured close to the pine plot. Soil moisture (θ_{0-30}) first measured weekly in the oak plot, then continuously. 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).

Water potentials

Minimum predawn leaf water potentials were *ca.* -0.8 and -0.9 MPa for oak and pine, respectively, but higher values were typically measured in oaks (Fig. 2). There were more differences between species in midday $\psi_{l,md}$, which was generally lower for oaks. Indeed, minimum $\psi_{l,md}$ was much lower for oaks (-3.2 MPa) than for pines (-2.1 MPa). The difference between oak $\psi_{l,pd}$ and $\psi_{l,md}$ clearly increased as the growing season developed

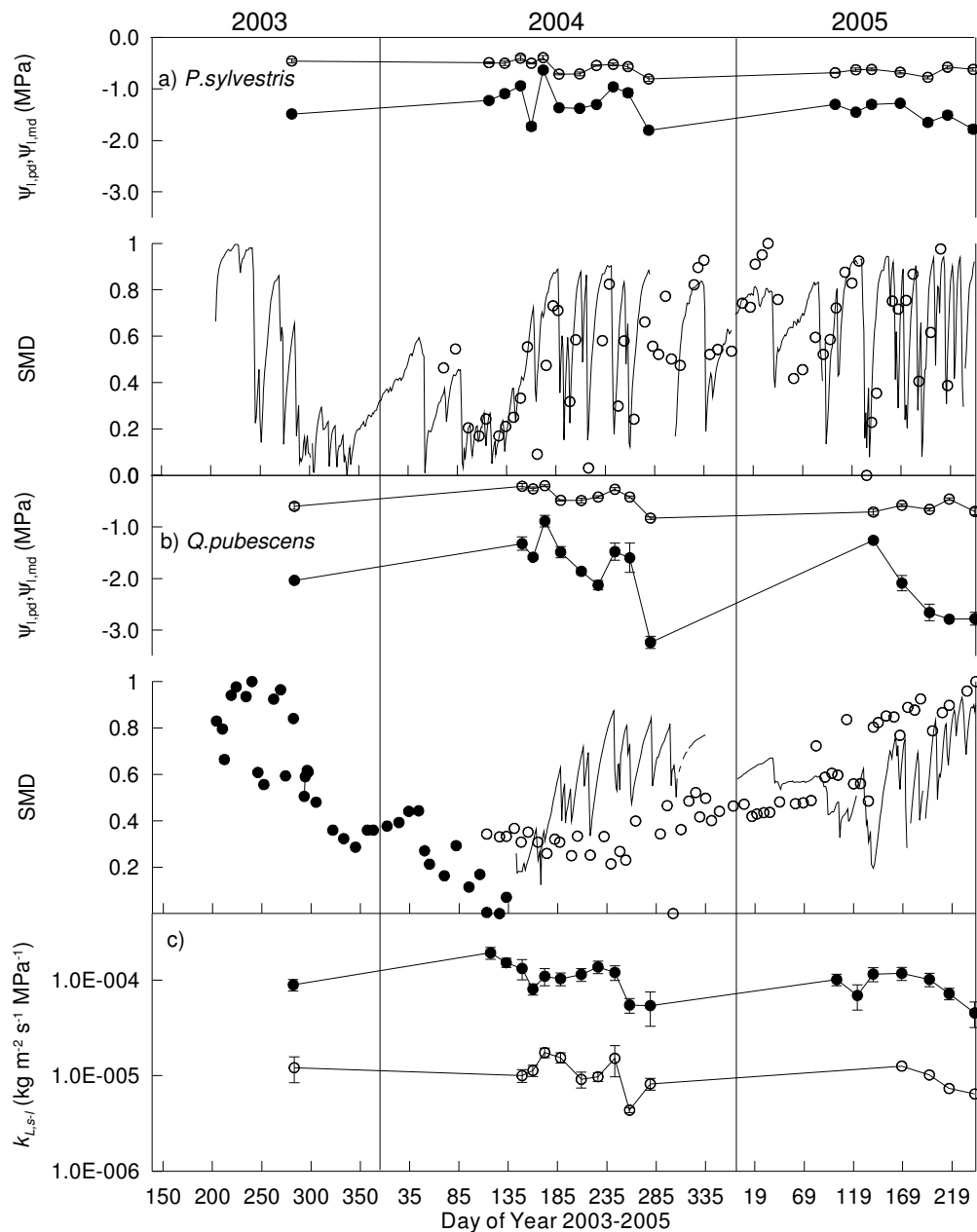


Figure 2. Seasonal evolution of predawn ($\psi_{l,pd}$, open symbols) and midday ($\psi_{l,md}$, closed symbols) leaf water potentials in *Pinus sylvestris* and *Quercus pubescens*, together with soil moisture deficit (SMD) values estimated at the two depths where soil moisture was measured (0-30 and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

for the measured dates in 2004 and 2005 (Fig. 2). This trend was also observed for Scots pine, but only in 2005. Midday water potential decreased more steeply with decreasing $\psi_{l,pd}$ in the oak plot (Fig. 3a), bringing about a greater increase in water potential difference with decreasing $\psi_{l,pd}$. Predawn leaf water potential was better related to θ_{0-30} in the oak plot, although the variation in $\psi_{l,pd}$ with θ_{0-30} could apparently be described by a common relationship across plots (Fig. 3c). However, an ANCOVA analysis revealed that there was not homogeneity between slopes in the linear relationship between log transformed $-\psi_{l,pd}$ and θ_{0-30} ($P < 0.001$).

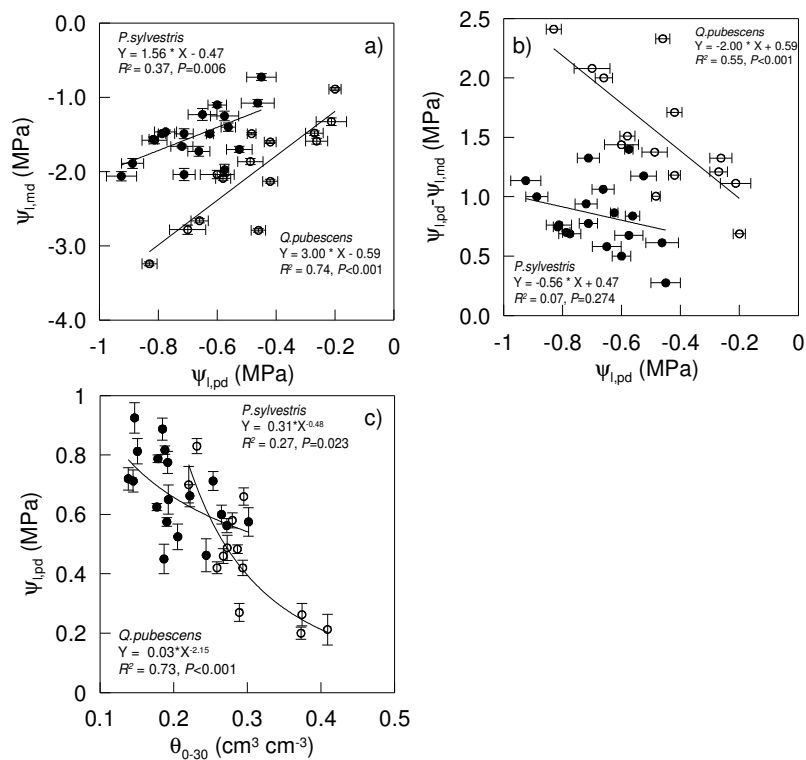


Figure 3. Relationships between (a) predawn ($\psi_{l,pd}$) and midday ($\psi_{l,md}$) leaf water potentials, (b) between water potential difference ($\psi_{l,pd} - \psi_{l,md}$) and (c) between $\psi_{l,pd}$ and soil moisture in the upper 30 cm (θ_{0-30}). Closed symbols represent data points for *P.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

Scaling of Scots pine sap flux density according to radial patterns

Sap flux density peaked at different depths within the sapwood depending on the tree, but in all cases the peak was located between the 3 mm and the 19 mm measuring points (data not shown). On average, the correction coefficients shows how sap flux density is quite uniform in the first 20 mm, where heat dissipation sap flow gauges are installed, and it starts to decline gradually beyond this point (Fig. 4). Whole-tree correction coefficients to convert single-point sap flux density into a radially weighted value ranged between 0.44 and 0.93, with an average value of 0.74.

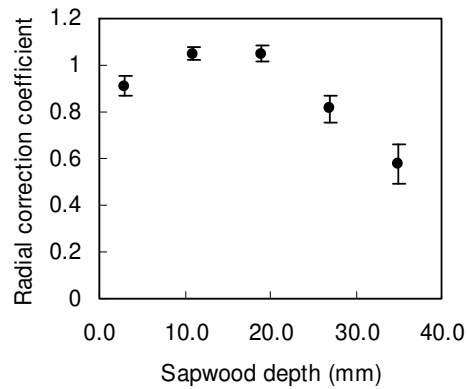


Figure 4. Coefficients employed to account for radial variations of sap flow. The mean value (\pm SE) of the measured trees is shown.

Sap flow and G_s responses to environmental variables

Relative sap flow 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. 5). Specially during the summer of 2003, the difference in the sap flow response between pine and oak was noticeable. Overall, sap flow relationships with D and R_n were similar for both species (Fig. 6). A marked decrease in relative sap flow with D above ca. 1.2 kPa was particularly appreciable during the year 2003 (Fig. 6a).

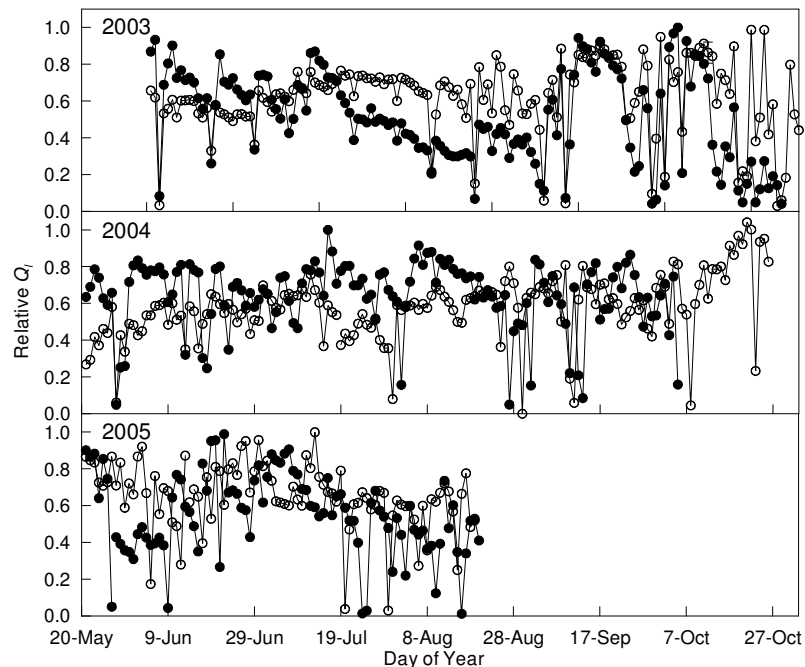


Figure 5. Seasonal evolution of sap flow per unit leaf area relative to its maximum value for *Pinus sylvestris* (closed symbols) and *Quercus pubescens* (open symbols) during the three years included in the study period.

A declining trend of relative sap flow with SMD_{0-30} was observed for Scots pine in 2003 and 2005, but not for 2004 (Figs. 6c,f,i). Only during 2005 a clear decline in oak relative sap flow with SMD_{0-30} could be observed (Fig. 6i). After omitting days with $D > 1.2$ kPa and $R_n < 200$ $W\ m^{-2}$, to avoid the interference high D and low light, we did not find significant linear relationships between relative sap flow and SMD_{30-60} (Year 2004, $N=12$, $R^2=0.26$, $P=0.093$; Year 2005, $N=7$, $R^2=0.44$, $P=0.079$) for Scots pine. Pubescent oak did not even show a declining trend in the variation of relative sap flow with SMD_{30-50} for the year 2004 (data not shown) but showed an apparent decline for 2005, which was not statistically significant ($R^2=0.55$, $N=4$, $P=0.256$).

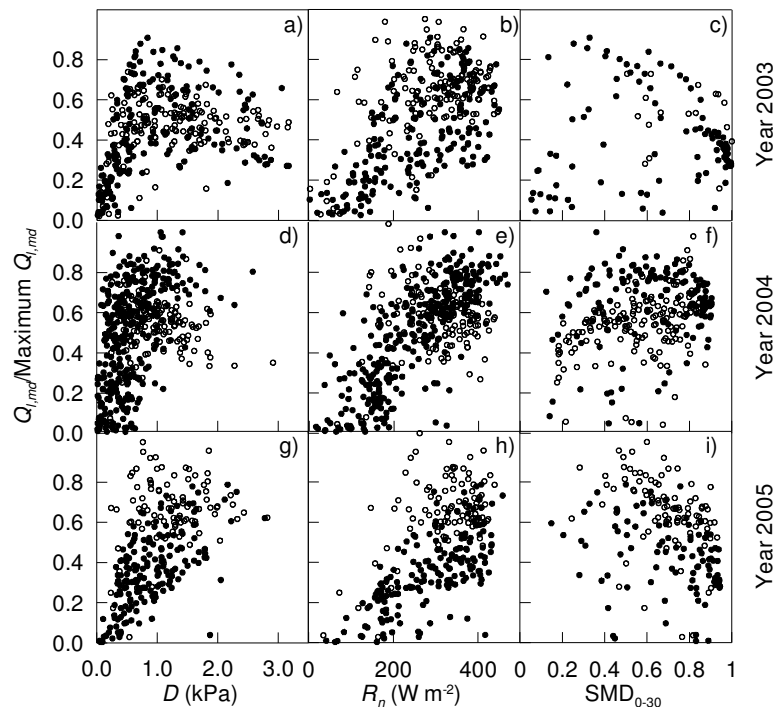


Figure 6. Relationships between relative sap flow and vapour pressure deficit (D) or net radiation (R_n), for *Pinus sylvestris* (closed symbols) and *Quercus pubescens* (open symbols).

A more detailed examination of meteorological conditions and the response of stomata to the increased water deficits during the summer of 2003 showed that the ratio of sap flow-derived canopy stomatal conductance at midday between pine and oak $G_{s,md}(\text{pine})/G_{s,md}(\text{oak})$, declined with extreme D and SMD conditions, meaning that, under such circumstances, $G_{s,md}$ in pine decreased proportionally more than in oak (Fig. 7). After substantial precipitation (> 40 mm), the subsequent refilling of soil water reserve cause pine $G_{s,md}$ to increase more than oak $G_{s,md}$, as revealed by the increase in the calculated ratio $G_{s,md}(\text{pine})/G_{s,md}(\text{oak})$ (Fig. 7).

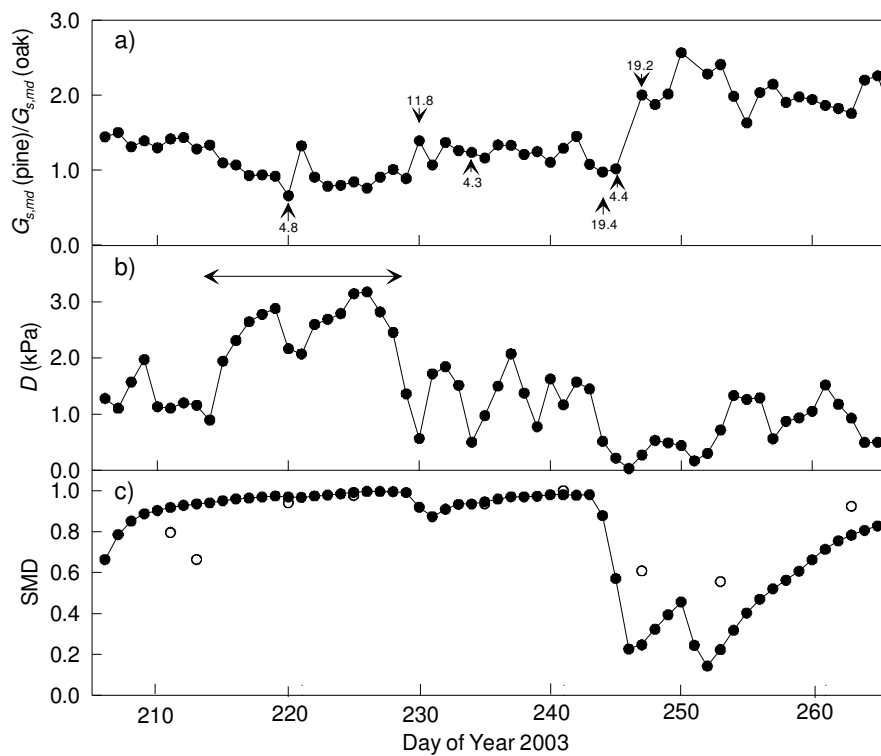


Figure 7. (a) Ratio between pine and oak midday canopy stomatal conductances ($G_{s,md}$), (b) the corresponding conditions of daytime-averaged vapour pressure deficit (D) and (c) soil moisture deficit in the upper soil layer (SMD_{0-30}) during the dry episode of the summer of 2003 and posterior recovery. The period with extreme D conditions is marked with an arrow. Arrow heads and numbers show rainfall amounts.

The values of $G_{s,md}$ were higher for Scots pine (Fig. 8a), according to its also higher rates of sap flow per unit leaf area. However, our data showed that beyond predawn values of -0.8 MPa, Scots pine $G_{s,md}$ would be reduced to 10% of its maximum value (Fig. 8a). Pubescent oak kept $G_{s,md}$ around 30% of its maximum within a range of leaf water potentials from -0.4 to -0.8 MPa (Fig. 8b).

Hydraulic conductance

Whole-plant hydraulic conductance on a leaf area basis ($k_{L,s-l}$) was generally more than an order of magnitude higher for Scots pine (Fig. 2). Scots pine showed lower ratios between water transpiring and conducting area. The calculated average values of leaf-to-sapwood area ratios ($A_L:A_S$) were $0.065 \text{ m}^2 \text{ cm}^{-2}$ and $0.121 \text{ m}^2 \text{ cm}^{-2}$ for pine and oak, respectively. During the year 2004, both species showed declining trends in $k_{L,s-l}$ during the central part of the summer and then recovered at the end, to decrease again at the beginning of autumn.

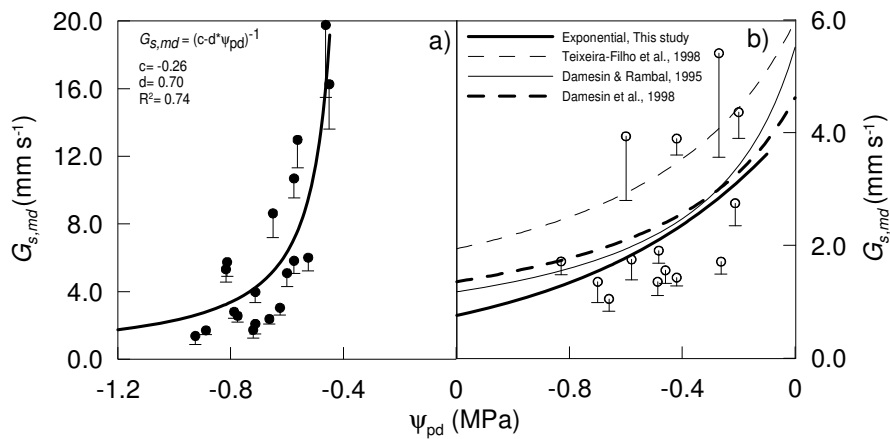


Figure 8. Midday canopy stomatal conductances ($G_{s,md}$) for *Pinus sylvestris* and *Quercus pubescens* related to the value of predawn leaf water potential. The fitted functions are based on Acherar and Rambal (1992), except for the exponential fit used for *Q.pubescens* data in the present study.

Spring values of $k_{L,(s-l)}$ for Scots pine were contrastingly different for 2004 and 2005. While the maximum value was attained in April 2004, typical mid-summer values of $k_{L,(s-l)}$ were found for the same month the following year. Then, as evaporative demand increased from mid-June 2005, $k_{L,(s-l)}$ declined in parallel for both species (Fig. 2).

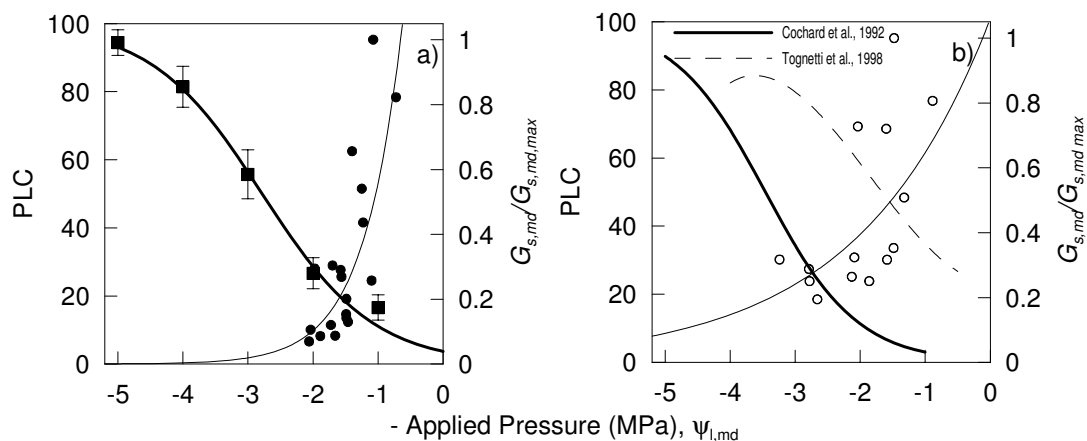


Figure 9. (a) Percent loss of hydraulic conductivity (PLC) for *Pinus sylvestris* branches with respect to the negative of applied pressure (MPa). The curve was fitted to all the individual measurements of PLC but closed squares are the average of PLC's calculated for $n=10$ branches. The variation of the ratio between midday canopy stomatal conductance ($G_{s,md}$) and its maximum value ($G_{s,md,max}$), and midday leaf water potential ($\psi_{l,md}$) is also shown for *P.sylvestris* (a) and for *Q.pubescens* (b). For the latter we plotted for comparison the two published vulnerability curves (Cochard et al., 1992; Tognetti et al., 1998).

The variation of $k_{L,(s-l)}$ was closely related to that of SMD_{0-30} for Scots pine. A negative linear relationship could be established between both variables ($R^2=0.46$, $N=19$, $P=0.002$), but not for *Q.pubescens* ($R^2=0.24$, $N=14$, $P=0.08$). However, this lack of fit was driven by the departure of two points from the apparent decreasing trend. Without these two points, which corresponded to dates very close to leaf unfolding (days 149 and 160), a much better fit resulted ($R^2=0.57$, $N=14$, $P=0.002$).

Vulnerability to embolism and relationships between hydraulic conductance and gas exchange

The parameters (nonlinear regression estimate \pm SE) of the vulnerability to embolism curve (Fig. 9a) 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 $K_W=4.4\cdot 10^{-4}$ m² wood area MPa⁻¹ s⁻¹ and $K_L=2.7\cdot 10^{-8}$ m² leaf area MPa⁻¹ s⁻¹, respectively. Combining the measured leaf water potentials and the information from the vulnerability curves, we observed that the maximum predicted PLC in the field approached 30%.

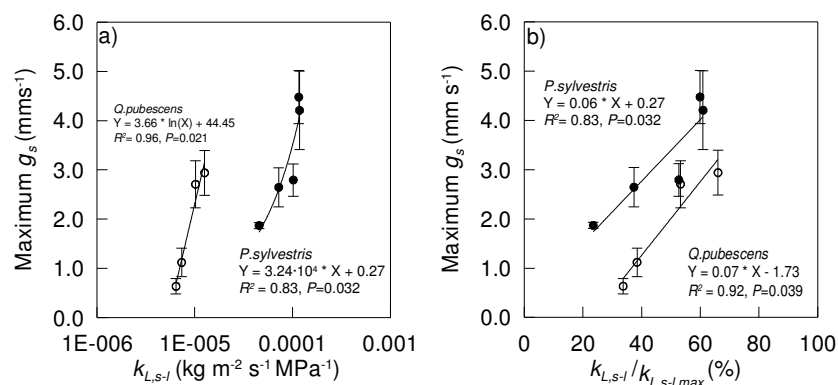


Figure 10. Relationship between and maximum stomatal conductance to water vapor measured at the leaf-level (g_s) and whole-plant hydraulic conductance ($k_{L,s-l}$), (a) expressed as absolute values and represented in a logarithmic scale and, (b) plotted as relative values. Closed symbols represent *Pinus sylvestris* and open symbols, *Quercus pubescens*.

Plotting the value of $G_{s,md}$ with respect to the maximum value of $G_{s,md}$ against the predicted loss of conductivity, *P.sylvestris* showed reductions of $G_{s,md}$ to less than 10% of its maximum value when leaf water potentials fell beyond -2.0 MPa, meaning a 30% of conductivity losses. The available information on *Q.pubescens* vulnerability to embolism (Cochard et al. 1992a; Tognetti et al. 1998) showed quite different results (Fig. 9b) and do not allow for a precise relationship between stomatal conductance and loss of conductivity (cf. Discussion). However, we could observe that *Q.pubescens* still maintained $G_{s,md}$ at 30% of its maximum value when leaf water potentials were lower than -3.0 MPa (Fig. 9b).

Finally, leaf-level stomatal conductance (g_s) was closely linked to measured hydraulic conductance in both species (Fig. 10), linearly for Scots pine and logarithmically for pubescent oak. In addition, a significant relationship was also established between Scots pine PLC predicted by the vulnerability curves and maximum g_s .

Discussion

Meteorology, soil moisture water potentials

Concurrent measurements of leaf water potential have shown that 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 (Damesin and Rambal 1995; Tognetti et al. 1998), the values found for Scots pine are among the lowest ever measured, with the exception of measurements taken in other populations in NE Spain (Martínez-Vilalta and Piñol 2002). Unfortunately, we did not measure water potentials during the 2003 summer drought, when the lowest values of leaf water potentials must have been reached.

Pre-dawn leaf water potentials never fell below -1 MPa in either species, and again, they were much higher than values measured elsewhere during dry periods (Martínez-Vilalta and Piñol 2002; Tognetti et al. 1998). Predawn water potential is often interpreted as being in equilibrium with the water potential of the wettest soil layer 'sensed' by the roots (Bréda et al. 1995). Predawn water potentials were more frequently higher for pubescent oak. This could indicate that oak is able to explore the soil adequately in search of water resources, extending taproots deeper in the soil or even in groundwater (Valentini et al. 1992), or simply be due to the finer texture of the soil in the oak stand. Regarding oaks in general, Rambal et al. (2003) found that ψ_{pd} measured in *Quercus ilex* L. decreased beyond a threshold in soil moisture measured over a depth of 450 cm and Bréda et al. (1995) found that *Quercus petraea* ψ_{pd} matched soil water potential measured at 140 cm depth.

Midday water potential decreased with decreasing ψ_{pd} for pubescent oak, therefore allowing a greater increase in the driving force for transpiration as edaphic drought developed. However, this driving force did not significantly increase with ψ_{pd} for *P.sylvestris*.

Sap flow and G_s responses to environmental variables

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, Scots pine showed higher relative sap flows (year 2004) but when dry periods occurred (in 2003 and 2005), the sensitivity of sap flow to superficial SMD at high was evident. 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 (Damesin and Rambal 1995; Nardini and Pitt 1999), even lower than the turgor loss point (Lo Gullo et al. 2003), while Scots pine efficiently closes stomata beyond a threshold in soil moisture (Irvine et al. 1998) and in response to high vapour pressure deficits (Beadle et al. 1985).

We found that $G_{s,md}$ decreased with ψ_{pd} in Scots pine, showing very reduced conductances (10% of the maximum value) when ψ_{pd} approached -0.8 MPa. It has been recently shown that, during an imposed drought experiment, the ratio between canopy conductance of droughted and control trees fell to 0.2 when minimum ψ_{pd} of -0.8 MPa were reached (Perks et al. 2002). Also Sturm et al. (1998) showed similar reductions of leaf-level g_s with decreasing ψ_{pd} . At the lowest measured ψ_{pd} , pubescent oak kept stomatal conductance at higher levels, about 30% of the maximum value. Although we could not fit the function proposed by Acherar and Rambal (1990) for *Q. pubescens* the exponential fit we obtained was close to the relationship fitted for the same species in southern France (Damesin and Rambal 1995). Despite that the absolute values of conductance were higher in another location in Portugal, the reduction with ψ_{pd} was similar to our findings (Teixeira-Filho et al. 1998).

Hydraulic conductance

Whole-plant hydraulic conductance calculated on a leaf area basis was more than one order of magnitude higher in Scots pine than in pubescent oak, because leaf-area based sap flow measured at midday was much higher in the former species. Our values of *P. sylvestris* $k_{L,s-l}$ are the highest found for this species to date, as maximum values of only $6.60 \cdot 10^{-5} \text{ kg m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ were reviewed by Becker et al. (1999). Measured $k_{L,s-l}$ for *Q. pubescens* have been only reported for saplings, showing values between 4.5 and $6.5 \cdot 10^{-5} \text{ kg m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ (Lo Gullo et al. 2003; Nardini and Pitt 1999). These values are similar to those measured in a related oak species *Quercus petraea* in another montane area of the Iberian Peninsula (Aranda et al. 2005).

Although Scots pine possesses the highest branch-level conductivities among the Pinaceae (Martínez-Vilalta et al. 2004), typical sapwood conductivities of pines are lower than those of deciduous oak species (Cavender-Bares and Holbrook 2001; Martínez-Vilalta et al. 2004), as occurs in general for conifers and angiosperms (Tyree and Ewers 1991). More specifically, published branch-level measurements of K_s in pubescent oak (Tognetti et al. 1999) are almost an order of magnitude higher than those found for Scots pine's maximum K_s in this study. However, Scots pine has a lower $A_L:A_S$, achieving a higher

hydraulic sufficiency. This compensation mechanism was proposed by Becker et al. (1999) to explain the similar hydraulic sufficiency observed between conifers and angiosperms. We have found that $k_{L,S-I}$ was negatively correlated with soil moisture for both species. High levels of $k_{L,S-I}$ in Scots pine were only reached during the mild spring of 2004, before soil moisture deficits developed, then a stable value was maintained throughout the summer. Further decreases in $k_{L,S-I}$ were observed as the summer progressed in 2005. Our data agree with the results by Irvine et al. (1998) who found that hydraulic resistance (inverse of conductance) increased significantly for trees under a drought treatment but was maintained essentially constant for control trees.

The decline in $k_{L,S-I}$ 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, hydraulic conductance measured at the whole-plant level declined up to 50% of its maximum value in the deciduous *Quercus petraea* (Aranda et al. 2005; Bréda et al. 1993). Consistent with these observations, a maximum of 40% loss of conductivity at the branch-level has been reported for pubescent oak (Lo Gullo et al. 2003; Nardini and Pitt 1999).

Vulnerability to embolism in Scots pine, hydraulic conductance and gas exchange

The studied Scots pine population was slightly more vulnerable to drought-induced embolism than other populations located in montane areas more to the south (Martínez-Vilalta and Piñol 2002). We showed how there was 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. (1998) also found increases in hydraulic resistance without significant xylem embolisms in the trunk, suggesting an increase in below-ground resistances with drought development.

We did not get a clear picture of the relationships between stomatal control and embolism in *Q. pubescens* because of the disparity in the measured vulnerability curves. According to Cochard et al. (1992a), at water potentials of -3 MPa, a 35% in PLC would correspond to a value of 0.3 in the fraction of maximum conductance. If the vulnerability curve by Tognetti et al. (1998) is used instead, this PLC approaches 80%. Still, curves measured in a closely related hybrid *Quercus subpyrenaica* (*Q. faginea* × *Q. pubescens*), yield a ψ_{50} of ca. -2.5 MPa, which lies just between the former estimations (-3.4 MPa and ca. -1.5 MPa, by Cochard et al. and Tognetti, respectively). Nevertheless, the relevance of stomatal closure in avoiding fatal embolisms has been suggested for *Q. petraea*, a related species occupying more mesic habitats than *Q. pubescens*, which showed a reduction in leaf-level stomatal conductance to 10% of its maximum value when ψ_l reached -2.8 MPa and the corresponding PLC was 30% (Cochard et al. 1996).

We also found a significant correlation between $k_{L,s-l}$ and independent measurements of maximum leaf-level g_s in both species as observed elsewhere for pine (Addington et al. 2004) and some angiosperm species (Nardini and Salleo 2000; Sperry et al. 1993), but still unreported for oaks. A linear relationship between g_s and $k_{L,s-l}$ has been suggested to be characteristic of isohydric species (regulate of 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) (Hubbard et al. 2001). While the results in this study would suggest isohydric and anisohydric behaviour for pine and oak, respectively, it is not clear whether linear versus curvilinear relationship represent isohydric versus anisohydric behaviour (Meinzer 2002).

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 (Zweifel et al. 2005). In general, other studies involving coexisting pine and oak species show that the latter has a lower threshold ψ_l for stomatal closure and a higher ψ_{pd} , meaning greater avoidance of soil water stress (Kolb and Stone 1999).

While the fact that two species with contrasting morphologies are able to coexist may suggest a significant functional convergence in plant responses to the environment (Meinzer 2003), extreme drought conditions will definitely affect more negatively the performance of the less 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). On the contrary, *Q.petraea* was less affected than companion species by the extreme 2003 summer drought in Central Europe (Leuzinger et al. 2005).

The distribution of both species in NE Spain support the view that pubescent oak is more adapted to drought. Pubescent oak can be found from pre-litoral to montane areas, while Scots pine is restricted to the latter. However, the present dominance of Scots pine in montane landscapes of the Eastern Pyrenees indicates that drought does not seem to have exerted a strong selective pressure so far. The increased incidence of extreme drought periods (Houghton et al., 2001) is likely to affect Scots pine more severely than pubescent oak, which can bring about significant changes at the landscape level.

Conclusions

We have shown that the overall response to water deficits of Scots pine and pubescent oak under equivalent climatic conditions are similar, but differences are evident when extreme soil moisture deficits and evaporative demand conditions occur. Pubescent oak shows higher predawn leaf water potentials, which could be due to the finer texture of the soil in the oak plot or be indicative of 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 other locations in NE Iberian Peninsula, but generally lower than the values found for oak. Although both species showed decreasing sap flows beyond a threshold D , 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 lower measured potentials. We also observed that Scots pine regulated stomatal aperture to avoid substantial stem xylem embolism as predicted by measured vulnerability curves. We could not reach the same conclusion with published vulnerability curves for pubescent oak, though. Finally, maximum leaf level gas exchange was closely related to hydraulic conductance on a leaf area basis for both species, confirming the suggested coordination between hydraulic characteristics and stomatal regulation.

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