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Transpiration of montane *Pinus sylvestris* L. and *Quercus pubescens* Willd. forest stands measured with sap flow sensors in NE Spain

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Abstract

Stand transpiration was measured during the 2003 and 2004 growing seasons using heat dissipation sap flow sensors in a Scots pine (*Pinus sylvestris* L.) and a pubescent oak (*Quercus pubescens* Willd.) forest located in a montane area of the Eastern Pyrenees (NE Spain). The first aim of the study was to assess the differences in quantitative estimates of transpiration (E_c) and the response to evaporative demand of the two stands. Over the studied period of 2003, characterised by a severe drought episode during the summer, the oak stand E_c was only 110 mm compared to the 239 mm transpired by the Scots pine stand, although the ratio of transpiration to reference evapotranspiration (E_c/ET_0) in the oak stand compares well with the expected values predicted for low leaf area index (LAI) oak forests in southern Europe. Scots pine showed a strong reduction in E_c/ET_0 as the drought developed, whereas pubescent oak was less affected by soil moisture deficits in the upper soil. As a second objective, and given the contrasting meteorological conditions between 2003 and 2004 summer periods, the interanual variability of transpiration was studied in the Scots pine plot. Rainfall during the summer months (June–September) in 2003 was almost 40% less than in the same interval in 2004. Accordingly, transpiration was also reduced about 25% in 2003. Finally, Scots pine data from 2003 and 2004 was used to calibrate a simple transpiration model using ET_0 and soil moisture deficit (SMD) as input variables, and implicitly including stomatal responses to high vapour pressure deficits (D_d) and soil water status.

1. Introduction

Given its importance in the hydrological cycle, transpiration of whole forest canopies has been experimentally measured in a wide range of environments, from boreal to tropical, using different methodologies. Upscaled leaf or branch-level measurements of gas exchange (e.g. Saugier et al., 1997) or sap flow (e.g. Granier et al., 1996; Čermák

et al., 2004), micrometeorological methods, such as the Bowen ratio energy balance (e.g. Denmead et al., 1993) or eddy covariance systems (e.g. Baldocchi et al., 1988; Köstner et al., 1992), and soil water balance approaches (e.g. Ladekarl, 1998) have been used to estimate stand-level transpiration rates from hourly to yearly time-steps. At larger spatial scales, transpiration of forested watersheds is best addressed using catchment water balance (e.g. Wilson et al., 2001).

Usage of thermal sap flow methods (Smith and Allen, 1996; Čermák et al., 2004) has become widespread in forest hydrology and ecophysiology, because they are relatively simple and inexpensive, can be used in non-homogeneous terrain (Martin et al., 1997) and permit separate estimations of the tree transpiration component of forest evapotranspiration (Wilson et al., 2000). They give information with high temporal resolution about physiological processes and, at the same time, allow for long-term recordings of transpiration (Oliveras and Llorens, 2001), accounting for intra- and interanual variability of forest transpiration (Bréda and Granier, 1996). However, upscaling from stem and branch level to obtain daily estimates of stand transpiration still gives rise to significant uncertainties, due to circumferential and radial variation in sap flow along the stem (Nadezhdina et al., 2002), estimation of sapwood depths (Čermák and Nadezhdina, 1998) or tree to stand extrapolation (Hatton and Wu, 1995).

Scots pine (*Pinus sylvestris* L.), largely distributed throughout the Eurasian boreal and temperate zone, is restricted in the Mediterranean basin to montane environments (Barbéro et al., 1998). Pubescent oak (*Quercus pubescens* Mill.) distribution in Spain delimits the sub-Mediterranean region, the transition between Eurosiberian and Mediterranean vegetation areas (Ceballos and Ruiz de la Torre, 1979). While the first species is considered as early successional due to its ability to colonize abandoned farmland and pastures, the latter is the climacic species in most montane areas.

Extensive spontaneous afforestation by Scots pine after the abandonment of the agricultural activities in the area (Poyatos et al., 2003), have raised an important concern about its possible hydrological consequences, given the role of forest canopies in controlling the hydrologic balance under Mediterranean conditions (Piñol et al., 1999)

and the reported decreasing trends in water yields after increases in forested cover (Sahin and Hall, 1996; Gallart and Llorens, 2004). Mediterranean montane regions get much more rainfall than lowland areas, and during the summer, it is largely in the form of short and intense events (Gallart et al., 2002). However, the high interanual climatic variability is responsible for the periodic occurrence of drought episodes which severely affect the response of some species to meet the evaporative demand.

This paper aims at (1) determining daily transpiration of the two most representative forest canopies of the montane stage in NE Spain during the growing season (2) identifying the different responses of the two species to the imposed evaporative demand, specially given the occurrence of a very dry summer period in 2003, (3) studying interanual variability of Scots pine transpiration, and (4) obtaining a simple parametrisation for modelling forest transpiration as a function of reference evapotranspiration and soil moisture deficit in the Scots pine stand.

2. Materials and methods

2.1. Study area

The two experimental plots are part of the Vallcebre research area (42°12′ N, 1°49′ E), located in the Eastern Pyrenees (NE Spain). Research on several ecohydrological subjects have been carried out in the area since the late 1980's. 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. Mudstone and limestone substrates are predominant, resulting in clayey-rich soils in the first case, and bare rock areas or thin soils in the latter (Gallart et al., 2002). Climacic vegetation in the area corresponds to the *Buxo-sempervirentis-Quercetum pubescentis* association, but most of the land was terraced and deforested for cultivation in the past, and then progressively abandoned during the second half of the twentieth century (Poyatos et al., 2003). The present landscape is mainly a mosaic of mesophilous grasslands of the *Aphyllantion* type and patches of

Scots pine, which colonised old agricultural terraces after their abandonment.

2.2. Experimental sites

The Scots pine (Cal Sort stand) plot is located in a rather young stand (the oldest trees are about 60 years old) overgrowing 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, personal communication). The oak plot (Cal Barrol stand) lies by the village of Vallcebre, at ca. 1100 m a.s.l., just 0.8 km apart from the pine plot. Unlike the pine stand, 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. Stand structure differs in both plots in terms of stem density and understorey cover, but they have very similar leaf area indices (Table 1).

2.3. Meteorology and soil moisture

The main meteorological variables were measured ca. 2 m above the two forest canopies (Table 2), except for global shortwave radiation and bulk precipitation, which were both measured in a meteorological station located in a grass-covered terrace by the pine plot. Reference evapotranspiration (ET_0) was calculated according to Penman-Monteith equation (Monteith, 1965) as described in Allen et al. (1998).

Soil moisture in the upper 30 cm was recorded continuously only in the Scots pine plot, calibrating the CS615 probe (Table 2) with weekly measurements of soil moisture taken with a TDR cable tester (Tektronix 1502C). Only weekly data was available in the oak plot, hence, a linear regression between these measurements and the continuous readings of the CS615 probe in the pine plot was used to have an estimate of soil

moisture seasonal evolution in the oak plot.

2.4. Sap flow measurements

Sap flow was measured with heat dissipation sensors made in our own laboratories according to Granier (1985, 1987). Briefly, these sensors consist of a pair of needle-like probes, usually 20 mm long, which bear a copper-constantan thermocouple in the middle of the needle. Both needles are covered by an aluminium tube to homogenize temperature along the length of the probe and inserted in the trunk, with a vertical separation of ca. 12 cm, the upper probe being heated at constant power. When sap moves upwards, the temperature difference (dT) between heated and unheated needles decreases, and during the night, under conditions of zero flow, dT is maximum. The sap flow index K is then calculated from this two temperature differences and empirically related to the average sap flow velocity along the probe (Granier 1985, 1987).

The length of the probes was 20 mm for Scots pine and 10 mm for pubescent oak. Sharp variations in *Q.pubescens* sap velocity with sapwood depth have been reported (Čermák and Nadezhdina, 1998; Čermák et al., 1998), which would lead to possible underestimations of average sap flow by the Granier probe due to the influence of large velocity gradients on the estimate of average sap flow along the probe (Clearwater et al., 1999). Shorter needles, which have already been successfully tested in other oak species (Granier et al., 1994), were used in this study in order to minimise these measurement error, as recommended by Clearwater et al. (1999). Sensors were installed at breast height in 12 trees per plot in May–June 2003, selecting the trees according to the diametric distribution (Granier et al., 1996). One sensor was inserted in the north-facing side of each tree and covered with reflective insulation to avoid the influence of natural temperature gradients in the stem. Temperature differences were recorded every 10 s and stored as 15 min average in a data logger (DT500, DataTaker, Australia).

Due to technical failure after installation, only 8 sensors were functioning in the Scots pine plot during the 2003 measuring period (days 154 and 289, June to mid-October).

The calibration empirically obtained by Granier (1985) was used in both species, after discarding the alternative calibration by Lundblad et al. (2001) for Scots pine, which resulted in abnormally high transpiration rates (data not shown). To integrate the measured sap flow velocity to an average sap flux density along the whole conducting sapwood, a correction factor which accounts for radial variation of sap flow in Scots pine has been applied (Köstner et al., 1996). In pubescent oak, no correction has been adopted and measured velocity in the outer 10 mm of sapwood has been extrapolated to the whole conducting area. Although this assumption may lead to an overestimation of the total flux (Nadezhdina et al., 2002), we will consider that it counteracts the effects of the previously mentioned underestimation of average sap velocity along the length of the probe.

2.5. Estimation of sapwood area and scaling up sap flow data to stand transpiration

A gravimetric analysis of wood cores was done to estimate sapwood depths in sample trees of both species. Cores from north and south aspects of the stem were extracted with a Pressler increment borer (Suunto, Finland) in 14 pines and 11 oaks during mid-August 2003. Sapwood was first visually identified in the field, and then taken to the laboratory, where volumetric fraction of water (f_w) was estimated in discs of about 4 to 10 mm in length, from outer to inner xylem (Kravka et al., 1999) to estimate radial variation in f_w. Sharp decreases in xylem water content usually indicate the boundary between conducting sapwood and non-conducting heartwood in conifers. After sapwood was identified in each sample tree, a regression was obtained between basal area (A_b) and sapwood area (A_s) of individual trees.

Stand transpiration (E_c) was then calculated adopting a diametric class stratification scheme (Köstner et al., 1992), by which each diametric class (5 cm increment) was assigned a corresponding sap flow density calculated from the averaging of all the trees measured within that class. Transpiration of each class relative to total stand transpiration, calculated during periods with all diametric classes being measured, was

used to fill the gaps whenever a diametric class was missing (i.e. due to sensor failure).

2.6. Analysis of the response of forest transpiration to evaporative demand

As a first approach, we analysed the relationship of E_c with ET_0 fitting a saturation curve as the one employed by Ewers et al. (2002)

$$E_c = a(1 - \exp(-b \cdot ET_0)) \quad (1)$$

In order to predict forest transpiration as a function of reference evapotranspiration and soil water status, a boundary-line analysis (Chambers et al., 1985) was first carried out between E_c and the natural logarithm of ET_0, with the purpose of finding an upper envelope on the data points, i.e. the relationship between E_c and ET_0 when there are no other limiting conditions. A quantile regression technique was used to find this optimal curve. This methodology, which was developed in econometrical analysis (Koenker and Basset, 1978), allows to fit a linear or nonlinear model to any desired quantile of a given data distribution. In ecological studies, this kind of analysis has proven very useful to detect relationships between pairs of variables when other factors, not included in the model, are known to be limiting the response of the dependent variable (Cade and Noon, 2003). We used the upper 95% quantile fit to calculate a maximum transpiration, under optimal soil moisture conditions ($E_{c,\max}$):

$$E_{c,\max} = a + b \cdot \ln(ET_0) \quad (2)$$

The ratio of actual E_c derived from sap flow and $E_{c,\max}$ was related to soil moisture deficit (SMD) using a nonlinear function

$$E_c/E_{c,\max} = 1 - k_1 \exp(-k_2 \, \mathrm{SMD}) \quad (3)$$

Where SMD is defined in the same way as in Granier and Loustau (1994),

$$\mathrm{SMD} = \frac{\theta_{\max} - \theta}{\theta_{\max} - \theta_{\min}} \quad (4)$$

with θ, θ_{min} and θ_{max} being actual, minimum, and maximum volumetric soil moisture ($cm^3\ cm^{-3}$) during the period of study, respectively. We split the 2003 and 2004 dataset of Scots pine transpiration, using the days with even Julian day for model calibration. To fit the soil moisture function, data points with daytime vapour pressure deficit (D_d) larger than 0.6 kPa were selected in order to minimise the likely errors in sap flow measurements and D_d under low evaporative demand conditions (Ewers and Oren, 2000).

Quantile regressions were performed with the statistical package R (R Development Core, Vienna, Austria) and parameter estimation in nonlinear regressions were obtained with SPSS (v.12.0., SPSS Inc., Chicago, USA).

3. Results

3.1. Individual tree sap flow results

Maximum instantaneous sap velocity (v_{max}), defined as the maximum 15 min recording, in *Q.pubescens* was ca. 2.5 dm h^{-1} whereas in *P.sylvestris* was about 1.5 dm h^{-1}. The average of measured v_{max} for each day increased linearly with stem diameter in Scots pine (Fig. 1a), but reached a plateau when the relationship with projected crown area was examined (Fig. 1b). No apparent trends with the abovementioned biometric parameters were found for *Q.pubescens* (data not shown).

Sap flow per unit of sapwood area in oaks remained higher than in pines during the studied period in 2003 (Fig. 2). Maximum sap flow density of 1200 l m^{-2} day^{-1} was recorded for *Q.pubescens* whereas *P.sylvestris* only reached 530 l m^{-2} day^{-1}. The dynamics was generally similar, apart from the late spring days, when a progressive increase in sap flow density was detected in oaks coinciding with a decreasing trend in pines.

3.2. Scaling-up to stand transpiration

Sapwood boundary delimitation based on steep declines in volumetric fraction of water in the xylem, as shown in Fig. 3a, was not always possible in *P.sylvestris*, and the visual determination from fresh wood cores was used instead. Sapwood depths ranged between 4.7 and 10.3 cm, extending to 70–80% of total xylem depth from cambium. Volumetric water content increased in depth along the xylem for *Q.pubescens* (Fig. 3b) and therefore the field estimation of sapwood depth was used also for this species. In some cases though, a decreasing trend of f_w with depth was initially observed in the first millimetres after cambium, followed by the abovementioned increase deeper in the xylem. Pubescent oak showed much narrower sapwood (1.4–2.8 cm deep), its extension varying between 15 and 40% of total xylem length for the biggest and smallest tree, respectively.

Regressions between basal (A_b) and sapwood area (A_S) showed that sapwood constitutes almost a constant 80% of the total basal area in Scots pine (A_s=0.80·$A_b^{1.01}$, R^2=0.996; the exponent is not different from unity, t-test, P=0.77), whereas in pubescent oak this proportion decreases with tree size (A_S=0.94·$A_b^{0.80}$, R^2=0.951).

3.3. Environmental variables and transpiration in pine and oak stands

Meteorological drivers of transpiration did not vary much between sites (Fig. 4). Net radiation and daytime vapour pressure deficit attained maximum values during the summer (ca. 400 Wm^{-2} and 3 kPa), with D_d largely below 1 kPa during late summer and early autumn. Minimum and maximum air temperatures were 7.2 and 27.1 °C respectively. Soil moisture in the upper horizons ranged between 0.16 and 0.32 cm^3 cm^{-3} in the pine plot and 0.19 cm^3 cm^{-3} and 0.31 cm^3 cm^{-3} in the oak plot. Scarce precipitations during the central part of the summer and high evaporative demand lead to rapid soil moisture depletion, only recovered after late summer rainfalls. Maximum transpiration rates in the Scots pine stand (3.7 mm day^{-1}) occured at the beginning of June, whereas for pubescent oak they took place in September (1.4 mm day^{-1}), after refilling

of soil water reserve. Leaf loss was observed in the Scots pine plot from mid-August, whereas no effects were appreciable in pubescent oak leaves during the 2003 summer drought.

The effects of limited water availability are already appreciable from the gradual decrease in relative transpiration (E_c/ET_0) of Scots pine from 8 July until 8 August, with values declining from 0.75 to only 0.25. In pubescent oak, relative transpiration was kept at an almost constant value of ca. 0.25 throughout most of the spring and summer, but increased gradually from mid-August to reach a value of ca. 0.50 at the end of the growing season. Days with E_c/ET_0 around 1 corresponded to very low D_d conditions (Fig. 4).

There was a more than two-fold difference between the estimations of canopy transpiration computed from June to mid-October of 2003 (Julian days 154-289) for both forest covers (Fig. 5). The Scots pine stand transpiration (239 mm) resulted to be higher than the amount of bulk precipitation (205 mm), and represented 46% of reference evapotranspiration (total ET_0=520 mm). Oaks transpired 110 mm, only 19% of the 592 mm estimated as ET_0 or 54% of cumulative rainfall.

3.4. Response of forest transpiration to evaporative demand

Daily canopy transpiration was clearly non-linearly related to reference evapotranspiration (Figs. 6a and 6b). At ET_0 lower than 3 mm day^{-1}, the response of both forest covers was roughly the same, independently from soil water conditions. However, at high SMD's and high evaporative demand (i.e. ET_0>3 mm) transpiration was substantially reduced in both cases (Figs. 6a and 6b). Sensitivity of canopy transpiration to ET_0, (Table 3) i.e. the parameter b in Eq. (1), was higher under severe drought conditions in Scots pine (t-test, P=0.004), but not in pubescent oak (t-test, P=0.058). This parameter differed between species only under drought conditions, though only marginally (t-test, P=0.020). Drought also significantly reduced parameter a in pubescent oak (t-test, P=0.001); only under these conditions parameter a differs between species

(t-test, P=0.000).

3.5. Interanual variability and modelling of Scots pine transpiration

The interanual comparison of transpiration in the Scots pine stand shows that, in 2004, the amount of water transpired into the atmosphere was ca. 80 mm higher than during the same summer period in 2003 (Table 4). Rainfall was substantially higher in 2004, about 40% more than in 2003, but the number of days with a developing water stress (SMD>0.6) was very similar for both years. However, severe water stress conditions (SMD>0.8) were much more common in 2003, together with dry atmospheric conditions (Table 4).

With respect to the transpiration model calibrated with 2003 and 2004 daily data, the results of the boundary-line analysis of E_c in relation to ET_0 yield an envelope curve which truly represents the response of the vegetation to the evaporative demand under optimal soil conditions (Fig. 7a). The subsequent analysis of the ratio between the estimated $E_{c,max}$ and soil moisture deficit reveals a strong limitation of transpiration when SMD>0.6 (Fig. 7b). The complete transpiration model (Table 5) was able to simulate relatively well the seasonal dynamics of transpiration (Fig. 8), although quantitative estimates were better for the 2004 measuring period. Modelled E_c for the period of 2003 with available soil moisture data (Julian days 205–289) was 160 mm, compared to 120 mm of measured E_c. In 2004, modelled E_c amounted to 314 mm, overestimating by ca. 15 mm the value obtained with stand-scaled sap flow measurements (Table 4).

4. Discussion

4.1. Individual tree sap flow and uncertainties in the upscaling to stand transpiration

Maximum instantaneous sap velocity measured in the outer xylem, defined as the maximum 15 min value for each day, was found to be within the limits reported in the literature for pines and oaks. Available data for Scots pine, indicates a range of v_{max} around

1–1.5 dm h^{-1} (Lundblad et al., 2001). To our knowledge, there is no published data on v_{max} for pubescent oak, but findings on very similar *Quercus* species (*Q. petraea*), show higher values of maximum sap velocity, around 2.8 dm h^{-1} (Bréda et al., 1993).

The positive relationships found in Scots pine between DBH and maximum sap velocity (Fig. 1) may be related to larger light availability in bigger trees, which also correspond with those in dominant positions within the stand. Stand-level transpiration estimates using a representative sap flow density for each diametric class is appropiate in this case, given the dependence of sap flow on tree size. In contrast, the much sparser oak stand would mean less competition for light and a lack of relationship between these variables. Accordingly, upscaling of individual sap flow measurements could have been addressed simply using mean sap flow density and multiplying by the ratio of sapwood to ground area ($A_S : A_G$), as sap flow was not dependant on tree size.

Mean sap flow per sapwood area increased during late spring in *Q.pubescens* and not in *P.sylvestris* (Fig. 2), probably due to the progressive development of earlywood vessels favouring water transport capacity (Bréda and Granier, 1996). Higher sap flow per sapwood area in *Q.pubescens* does not result in higher stand transpiration rates, due to the inferior conducting area in the oak plot compared to the value found for the pine plot (Table 1). Woody species bearing vessels with ring-porous anatomy usually have less sapwood area but higher sap velocities, contrarily to what happens in conifers (Swanson, 1994).

Non-uniformity of sap velocity in tree stems is one the most challenging issues in the upscaling process of sap flow measurements. Radial variation in sap flow of *P.sylvestris* stems has been documented in a number of works, reporting a Gaussian profile (Köstner et al., 1996; Nadezhdina et al., 2002). The correction coefficient used in this work was also found from a Gaussian-like variation of sap flow along the xylem, being the best option to account for radial variability without actual measurements in the individuals from the studied stand. Recently, this Gaussian pattern has been generalized for conifers (Ford et al., 2004).

Uncertainties arising from not accounting for this variability have been found to be

higher in ring-porous species, with much sharper profiles of sap velocity, which means that only the outer growth rings actually contribute to water transport (Granier et al., 1994). The use of shorter probes in *Q.pubescens* was aimed at avoiding large gradients within the probe, which might have led to significant error measurements (Clearwater et al., 1999). Application of published radial profiles of sap flow for *Q.pubescens* (Čermák and Nadezhdina, 1998; Čermák et al., 1998) was refused because they show more variable shapes among individuals. In addition, the overestimation that theoretically should result from considering the outer xylem sap velocity as constant along the entire sapwood of pubescent oak (Nadezhdina et al, 2002), does not suppose very high values of canopy transpiration, on the contrary, the observed values of transpiration are lower than in other oak stands with similar structure (Bréda and Granier, 1996). It is possible, that, given the large radial sap flow gradients in this species, uncertainties derived from averaging sap flow density within the probe (Clearwater et al., 1999) and lack of sensitivity at high sap velocities (Lundblad et al., 2001), might counteract the effects of the abovementioned overestimation of transpiration. For example, David et al. (2004) have recently found that the variation in sap velocity in a *Quercus rotundifolia* Lam. tree did not significantly affect the estimation of whole-tree sap flow.

Finally, sapwood delimitation is also a likely source of error in transpiration estimates from sap flow measurements. Whereas its distinction from differences in wood moisture content is recommended in conifers (Rust, 1999), measured radial profiles of sap flow have been strongly recommended to delimit sapwood in oak species (Čermák and Nadezhdina, 1998).

4.2. Differences in stand-level transpiration between pine and oak forests

Maximum stand transpiration rates measured for *P.sylvestris* lie near the upper limit for 20 to 60 year-old conifer stands, ca. 3.9 mm (Moore et al., 2004). Estimates of stand transpiration in other similar Scots pine stands from central and northern Europe are certainly lower than the values found in this study. Growing season values range from less than 100 mm (Lüttschwager et al., 1999) to an upper limit around

300 mm (Jaeger and Kessler, 1996), the latter figure obtained as a long-term average. Modelling approaches yield values of yearly transpiration of about 230 mm in a Belgian stand (Meiresonne et al., 2003) or intervals for southern Europe forests between 200 and 450 mm year^{-1} (Berninger, 1997). Our results are more comparable to other Mediterranean pine forests. For example, Loustau et al. (1996) estimated a total transpiration of 194 mm between June and August in a *Pinus pinaster* Ait. forest in Portugal (compare with the values in Table 3).

The low seasonal E_c/ET_0 value found for the oak forest is slightly lower than the one predicted using the equation relating transpiration to potential evapotranspiration with LAI in *Quercus petraea* forests (ca. 0.25) in southern France (Bréda and Granier, 1996). Likewise, in a *Q.pubescens* forest in Italy with a considerably higher leaf area index (LAI=3.8 m^2 m^{-2}), Čermák et al. (1998) found that E_c (214 mm in total, between May and October) was about 29% of ET_0 during the whole growing period, compared to 19% in this study. In view of these results, the combination of a lower LAI and the occurrence of a exceptionally dry summer may be responsible for the inferior E_c/ET_0 in our stand.

Water balance components for the studied period of 2003 reveal a very tight hydrological budget in the case of Scots pine. If we apply the bulk rainfall interception rates found in a similar nearby stand (24% of bulk precipitation; Llorens et al, 1997), net rainfall amounts to only ca. 150 mm, and therefore fails to supply the amount of water transpired by the stand. Depletion of deep soil water and removal from stem storage (Waring et al., 1979) to meet the evaporative demand may have accounted for this difference. For instance, during the Julian days 214 to 228 (first half of August), when drainage can be assumed negligible, soil water balance in the upper 30 cm of the soil yielded estimates of evapotranspiration that were only 12–25% of the E_c measured with sap flow sensors (data not shown). Unlike the Scots pine stand, bulk rainfall largely exceeded transpiration in the oak stand. Interception rates in similar oak forests in NW Spain (ca. 15% of rainfall; Moreno et al., 2001) are lower than the value found for Scots pine, but understorey interception and litter evaporation components may also be im-

portant (Wilson et al., 2000). In addition, undestorey transpiration in the oak forest must account for a significant fraction of ecosystem evaporation. Čermák et al. (1998) found in a similar oak stand, with higher LAI (see this section), that understorey transpiration was ca. 15% of total stand transpiration (understorey plus overstorey). Therefore, the complete water balance would require some estimation of below canopy processes.

The higher reduction in matching the evaporative demand in Scots pine in comparison to pubescent oak (Fig. 4) is in accordance with the present ecophysiological knowledge on both species. Whereas Scots pine has a strong stomatal control of transpiration under atmospheric and edaphic drought (Irvine et al., 1998), pubescent oak can stand lower water potentials and can be regarded as more drought-tolerant (Nardini and Pitt, 1999; Zweifel et al., 2005). Extreme drought episodes have been found to produce more negative effects on the performance, and even the survival of Scots pine (Martínez-Vilalta and Piñol, 2002) than on other temperate deciduous oak species (Leuzinger et al., 2005).

4.3. Interanual variability and modelling of Scots pine transpiration

In Mediterranean mountain areas, summer storms usually buffer the effects of high evaporative demands, but these precipitations are highly variable both in time and space (Gallart et al., 2002), bringing about also a high variability in forest transpiration. Rainfall between June and September of 2003 (Table 4) was well below the long-term average value of ca. 330 mm (Latron, 2003). More specifically, precipitation between June and August of 2003 (111 mm) was much less than the value recorded in 1998 (159 mm), considered an extremely dry year in NE Spain (Martínez-Vilalta and Piñol, 2002). This figures confirm the effects of the 2003 heat wave (Schär et al., 2004) on rainfall amounts in northern Spain. Despite that 2004 was much milder from the meteorological point of view, a moderate depletion of the upper soil layers still occurred (Table 4) which indicates that trees intensively extract water from the upper 30 cm of soil during an average year.

Transpiration dynamics was successfully modelled using only reference evapotran-

spiration and soil moisture deficit as inputs in the Scots pine stand, although it was generally overestimated (Fig. 8). Despite that the most employed approach of modelling forest transpiration is the implementation of a canopy conductance model in the Penman-Monteith equation (e.g. Stewart, 1988), the model we used implicitly incorporates the well-known stomatal closure at high vapour pressure deficits (Oren et al., 1999), as the relationship between $E_{c,\max}$ and ET_0 is logarithmic. The observed reduction in E_c due to soil water stress is also similar to other functions found in the literature (Lagergren and Lindroth, 2002), showing a soil moisture deficit threshold beyond which transpiration is strongly limited. There are some drawbacks, however, in using this simple model. Leaf area index is not included in the model and hence it should be used in similar forest stands, and also, this approach is not as suitable to detect between-species differences in stomatal regulation due to vapour pressure deficit or soil moisture as, for example, the widely used Jarvis-type conductance model (Jarvis, 1976). However, data from sap flow experiments or flux towers could be used in similar parametrisations for different kinds of forests. Soil moisture deficit was derived in this work from actual soil moisture measurements, although similar indices could be obtained solely from rainfall inputs (Oren and Pataki., 2001).

5. Conclusions

Transpiration in a montane Scots pine forest in NE Spain was twice the value found for a nearby pubescent oak stand. Higher sap velocities in the oak stand could not compensate for the more than threefold difference in sapwood area with respect to the pine stand. The existing uncertainties in upscaling sap flow in ring-porous oaks could explain the differences in transpiration estimates. At the ecosystem level, though, a greater contribution of understorey transpiration and evaporation is expected in the oak stand.

Scots pine was found to be more sensitive to soil drought in the upper soil layers because of its strong reduction in the response to atmospheric forcing, while pubescent

oak transpiration was kept at a relatively constant fraction of evaporative demand during the dry summer period. These results confirm the general physiological behaviour of both species under drought conditions. The similar frequency of moderate soil moisture deficits (SMD>0.6) in the upper soil horizons during an average and a very dry summer, is indicative that the threshold of soil moisture which limits water extraction by Scots pine is usually reached in these Mediterranean mountain forests.

Finally, the use of the boundary-line analysis with the quantile regression method yielded a satisfactory logarithmic relationship of Scots pine E_c against ET_0, representing the stomatal closure at high vapour pressure deficits, and, further combined with a soil moisture function, allowed us to calibrate a simple transpiration model only dependent on evaporative demand and soil water status.

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Table 1. Stand characteristics of the *Pinus sylvestris* and *Quercus pubescens* experimental plots. DBH is diameter at breast height, $A_S : A_G$ is sapwood area per ground area and LAI_{max} is maximum leaf area index.

	P.sylvestris	*Q.pubescens*
Density (trees ha^{-1})	2165	828
DBH (cm)	15.2±5.8*	21.1±7.4*
Basal area (m^2 ha^{-1})	44.7	32.5
Height (m)	11.0±1.4*	10.6±2.8*
LAI_{max} (m^2 m^{-2})	2.4	2.1
A_S:A_G (m^2 ha^{-1})	37.0	9.7

*mean ± standard deviation.

Table 2. Measured atmospheric and soil variables and their corresponding sensors in the studied plots.

		P.sylvestris	*Q.pubescens*
Variable	Abbreviation and units	Sensor	
Air temperature Relative humidity	T (°C) RH (%)	HMP35AC, Vaisala (Vantaa, Finland)	HMP35C, Vaisala (Vantaa, Finland)
Net radiation	R_n (W m^{-2})	NR-Lite, Kipp & Zonen (Delft, The Netherlands)	
Wind speed	u (m s^{-1})	A100R, Vector Instruments (Rhyl, UK)	
Wind direction	degrees		6504, Unidata (O'Connor, Australia)
Soil moisture	θ (cm^3 cm^{-3})	CS615, Campbell Scientific (Leicestershire, UK)	
Soil temperature	T_{soil} (°C)	Termsistor	
Precipitation	P (mm)	Tipping Bucket Pluviometer AW-P, Institut Analític (Barcelona, Spain)*	
Global shortwave radiation	R_g (W m^{-2})	SP110 Pyranometer, Skye Instuments (Powys, UK)*	

* Installed in the catchment's general meteorological station.

Table 3. Parameters of the E_c–ET_0 curve (Eq. 1) under different soil moisture regimes (Fig. 6). 95% confidence intervals are shown between brackets.

	SMD	a	b	R^2
P.sylvestris	< 0.8	5.18** (1.35, 9.00)	0.16* (0.01, 0.31)	0.85
	> 0.8	1.49** (1.34, 1.65)	0.62** (0.35, 0.88)	0.44
Q.pubescens	< 0.8	1.49** (1.20, 1.79)	0.42** (0.26, 0.58)	0.84
	> 0.8	0.96** (0.90, 1.03)	0.68** (0.46, 0.89)	0.56

t-test significance levels: ** $p<0.01$; * $p<0.05$.

Table 4. Comparative amounts of transpiration (E_c), reference evapotranspiration (ET_0) and precipitation (P) in the Scots pine stand for the periods comprising days 154–274 (June to September) of 2003 and 2004. Percentage of days with high vapour pressure deficits (D_d) and soil moisture deficits (SMD) are also shown.

Year	Totals			Evaporative fractions		% of days with		
	E_c	ET_0	P	E_c/ET_0	E_c/P	D_d >1.5 kPa	SMD>0.6	SMD>0.8
2003	220	493	186	0.45	1.18	36	68	52
2004	299	460	298	0.65	1.00	8	64	31

Table 5. Parameters of the transpiration model (Eqs. 2, 3) and their correspondent 95 % confidence intervals (between brackets). For parameters obtained through quantile regression, 90% confidence interval is shown.

	a	b	k_1	k_2
P.sylvestris	1.34 (1.22, 4.03)	1.25 (−0.10, 1.38)	$1.22 \cdot 10^{-3}$ ($-1.95.10^{-3}$, $2.63.10^{-3}$)	6.23** (5.07, 7.52)

t-test significance levels: ** $p<0.01$; * $p<0.05$.

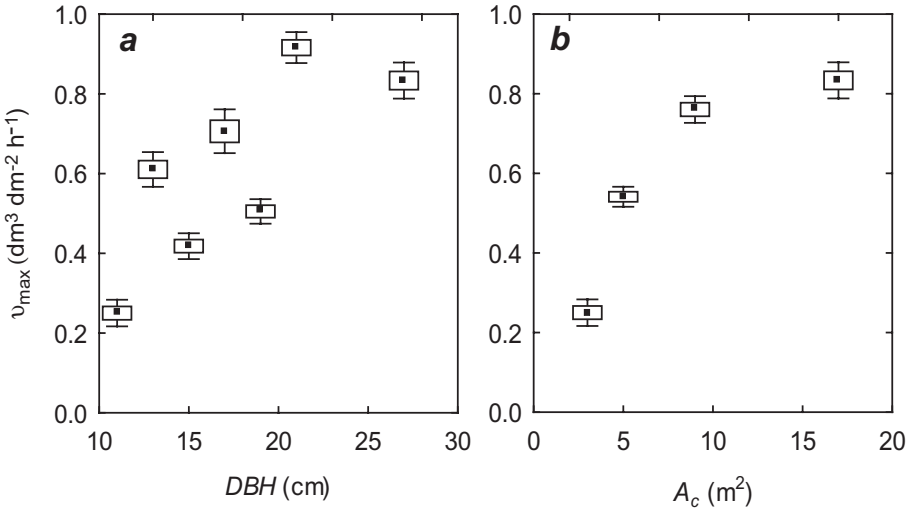

Fig. 1. Relationship between maximum sap velocity (v_{max}) and **(a)** DBH and **(b)** crown projected area (A_c) for *P.sylvestris*. Individual trees are grouped in integer categories of the independent variable. Points are means, boxes are standard errors and whiskers are 95% confidence intervals.

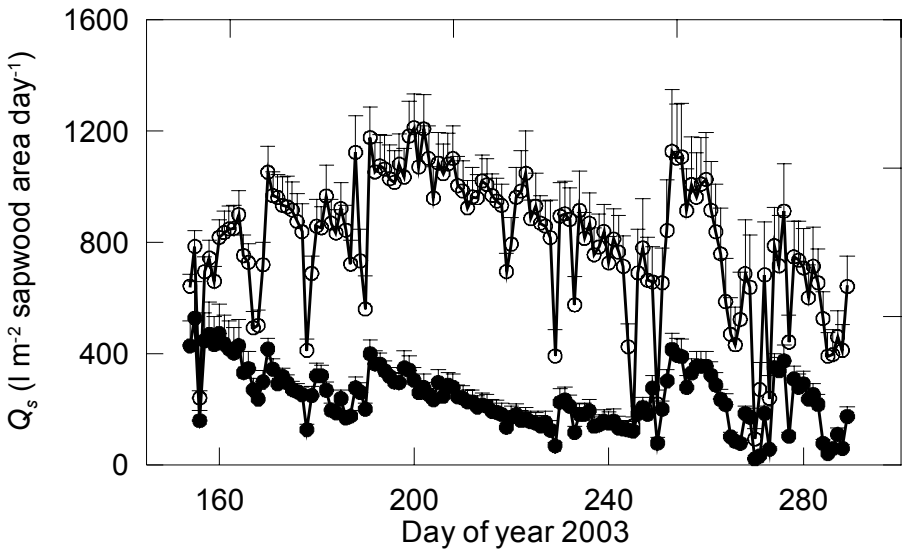

Fig. 2. Seasonal evolution of sap flow per sapwood area (Q_s) in *P.sylvestris* (closed symbols) and *Q.pubescens* (open symbols), showing the mean value of the individual trees plus one standard error.

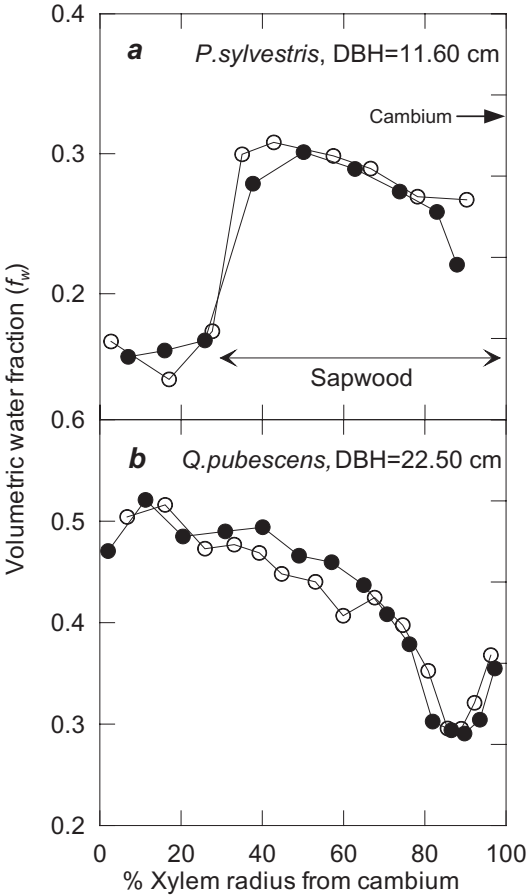

Fig. 3. Examples of fractional volumetric water content variation with depth in **(a)** *P.sylvestris,* showing identification of conductive sapwood, and **(b)** *Q.pubescens.* Closed and open symbols represent norh and south-facing cores, respectively.

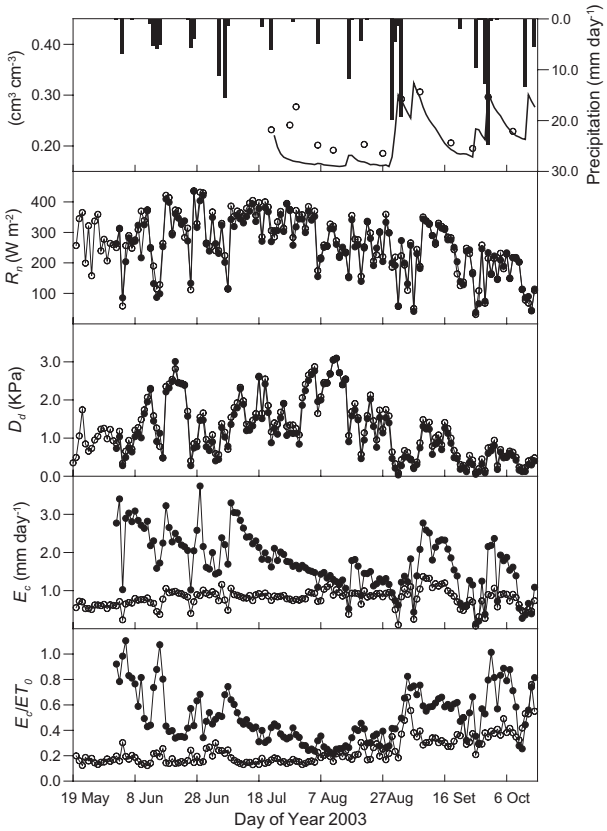

Fig. 4. Seasonal evolution of environmental variables and canopy transpiration of Scots pine (closed symbols) and pubescent oak (open symbols). R_n is net radiation, D_d daytime vapor pressure deficit, E_c stand transpiration, E_c/ET_0 relative transpiration and θ is soil moisture in the upper 30 cm. Daily soil moisture is shown for the pine plot (full line) and weekly values for the oak plot (open symbols).

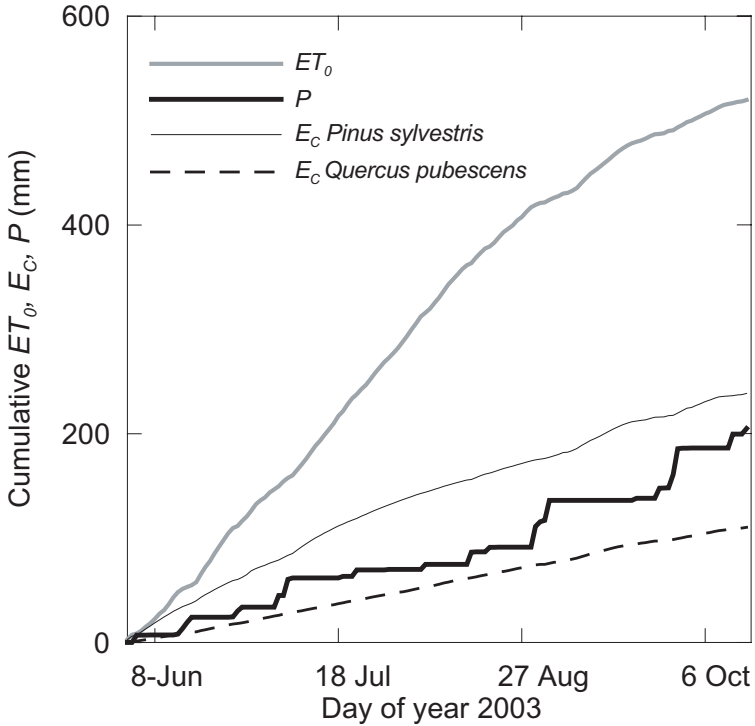

Fig. 5. Cumulative values of precipitation (P), stand transpiration (E_c) and reference (ET_0)evapotranspiration during the studied period in 2003 for the Scots pine and the pubescent oak stands. ET_0 is only shown for the Scots pine plot.

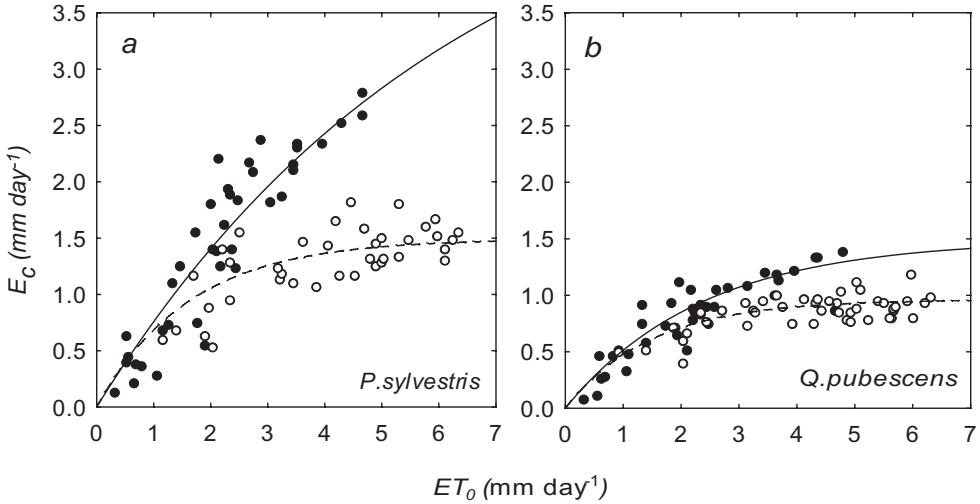

Fig. 6. Relationship of canopy transpiration E_c and reference evapotranspiration ET_0 under different soil moisture regimes (SMD<0.8, closed symbols, and SMD>0.8, open symbols), for Scots pine **(a)** and pubescent oak **(b)**. For fitted curves and parameter values see Table 4.

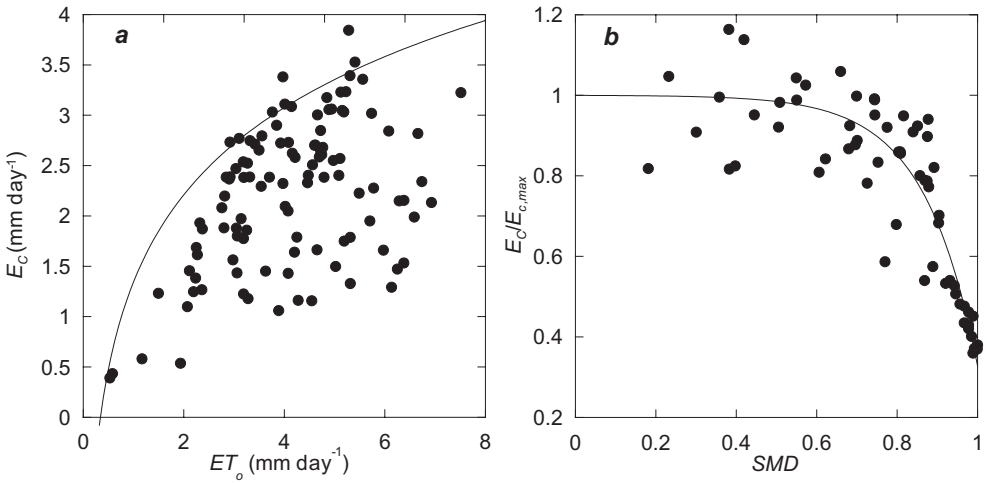

Fig. 7. Calibration of the transpiration model for Scots pine (Eqs. 2 and 3), showing data points and fitted curves. **(a)** Boundary line relationships of E_c against reference evapotranspiration ET_0 and **(b)** derivation of the soil moisture function.

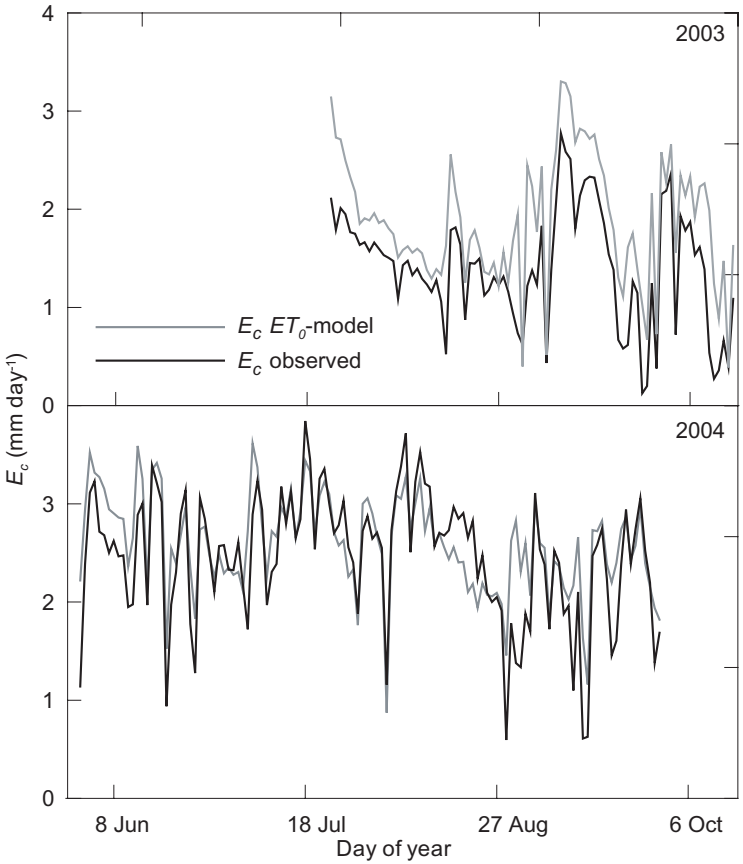

Fig. 8. Seasonal course of measured daily *P.sylvestris* stand transpiration (E_c) from sap flow measurements and modelled E_c during 2003 and 2004 study periods.