Original article

Retrieving leaf conductances from sap flows in a mixed Mediterranean woodland: a scaling exercise

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Abstract – Xylem sap-flux densities were monitored continuously using Granier-type sensors on five *Quercus ilex*, four *Arbutus unedo* and one *Quercus pubescens* from June 1993 to October 1994. Half-hourly measurements of incoming solar radiation, air temperature and humidity, horizontal wind speed and precipitation were carried out at the top of a tower at a height of 12 m, about 2 m above the canopy. Leaf physiological measurements (stomatal conductance, water potential) on individual sunlit leaves from each of the three tree species were obtained on seven complete or partial diurnal time courses. For these three species, to estimate leaf stomatal conductance, we used the big-leaf approach of Penman-Monteith. We have divided the leaves into sunlit and shaded. The model sums the individual-leaf model for only the sunlit fraction to produce the whole-canopy predictions. Transpiration was deduced from sap flux through a transfer function taking into account stem water storage. Stomatal conductance for a given species was evaluated half-hourly from transpiration and microclimate data inverting the Penman-Monteith equation. An empirical model was identified that related stomatal aperture to simultaneous variations of microclimate and plant water potential for the 1993 period. The predicted leaf conductances were validated against porometer data and those of the 1994 period. The diurnal patterns of predicted and measured transpiration indicated that stomatal conductance was accurately predicted. The leaf conductance models were also compared with already published literature values from the same tree species. In spite of the simplifications inherent to the big-leaf representation of the canopy, the model is useful for predicting interactions between Mediterranean mixed woodland and environment and for interpreting H_2O exchange measurements. (© Inra/Elsevier, Paris.)

mixed Mediterranean woodland / stomatal and canopy conductances / Penman-Monteith equation / sap flow / *Quercus ilex* / *Quercus pubescens* / *Arbutus unedo*

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Résumé – Estimation des conductances foliaires à partir des flux de sève dans une forêt mixte méditerranéenne : un exercice de changement d'échelle. La densité de flux de sève a été mesurée en continu à l'aide de capteur de type Granier sur cinq *Quercus ilex*, quatre *Arburus unedo* et un *Quercus pubescens* de juin 1993 à octobre 1994. Ces mesures ont été complétées par des mesures microclimatiques bihoraires de rayonnement global, de température et d'humidité de l'air, de vitesse du vent et de hauteur de précipitation. Ces mesures sont faites au sommet d'une tour de 12 m dominant le couvert forestier d'environ 2 m. Sept suivis journaliers complets ou partiels de conductance stomatique et de potentiel hydrique pour des feuilles exposées au soleil des trois espèces d'arbre ont été réalisés. Pour ces trois espèces, nous avons estimé la conductance stomatique à l'aide du modèle simple feuille de Penman-Monteith. Les feuilles sont subdivisées en feuilles de lumière et d'ombre. Seule les feuilles de lumière sont supposées contribuer à la transpiration totale. La transpiration est dérivée des mesures de flux de sève à l'aide d'une fonction de transfert qui tient compte du stockage de l'eau dans le tronc. La conductance stomatique est déduite de l'inversion du modèle de Penman-Monteith compte tenu de la transpiration et des conditions microclimatiques. Un modèle empirique multiplicatif de ces conductances a été ajusté sur les données acquises en 1993. Il les relie aux conditions microclimatiques et au potentiel hydrique foliaire. Ce modèle de conductance a été validé à l'aide des données acquises en 1994 et à des mesures de conductances réalisées au poromètre. Ce modèle a été comparé aux modèles de la littérature proposés pour ces espèces. En dépit des simplifications inhérentes à la représentation simple feuille du couvert, ce modèle est utile pour prédire les interactions entre les forêts mixtes méditerranéennes et leur environnement et pour interpréter les mesures de transpiration. (© Inra/Elsevier, Paris.)

forêt mixte méditerranéenne / conductances stomatique et de couvert / équation de Penman-Monteith / flux de sève / *Quercus ilex* / *Quercus pubescens* / *Arbutus unedo*

1. INTRODUCTION

Modelling terrestrial ecosystem functions at watershed, region or larger scales demands the development of generalized representations of the most relevant ecological and biophysical processes. Mass and energy exchanges in forest canopy are key factors in photosynthesis, net primary production, growth and some ecosystem functions and regional forest canopy physiology may influence climate and hydrological cycle. The links among canopy physiology, surface energy exchange, and water and carbon dioxide exchanges have been long recognized. Some models explicitly include this linkage [2, 3]. As emphasized by Bonan [6]: "A future challenge (...) is not to merely show that climate change affects terrestrial ecosystems, but rather to considered what level of physiological and biophysical detail is needed to accurately model climate change impact".

Measurements and modelling are difficult in the mixed evergreen canopies that are very common in Mediterranean landscapes. In these areas, natural vegetation has to cope with a strong seasonality in environmental conditions where cold wet winters alternate with hot dry summers. However, it is probably drought that has most dramatically shaped vegetation and controlled plant functions. If attempts are made to study mass and energy exchanges or even water yield of forested watersheds, one must take into account the interactions between soil or plant status, atmosphere and leaf regulation. This control can be considered at different time-scales. Scaling from leaf to canopy is not only a problem of changing spatial scale but also a problem of integrating temporal scales. Scaling is used here in the Norman [46] sense, i.e. "scaling implies an intuitive leap that provides a quantitative connection between distant phenomena – a short cut".

To the extent that is possible, measurements at different time and spatial scales are necessary to validate modelling scaling efforts. A continuous sap flow and leaf ecophysiology measurement program was conducted in a Mediterranean woodland. These data link the local scale environmental conditions with micro-scale leaf functioning, and consequently afford the opportunity to propose and test a model of canopy physiology. In this context, the big-leaf approach of Penman-Monteith [44] provided, if not quantitatively at least conceptually, a useful simplified description and the basis to explore stomatal effects on canopy transpiration with respect to tree species. The present study was undertaken to: 1) examine tree xylem sap flow and stomatal responses in a mixed evergreen Mediterranean woodland; 2) derive canopy conductance values from the inversion of the Penman-Monteith equation; and 3) identify and validate a multi-constraint empirical model of leaf conductance for each tree species.

2. SITE DESCRIPTION AND METHODS

2.1. Site description

The study site was located in the Peyne watershed about 45 km west of Montpellier, southern France (43°34' N 3°18' E, elevation 186 m) at the bottom of a south eastern facing 35 % slope. The woodland, composed of resprouted trees following a clear cut in 1945, has reached a height of ca 10 m and supports a leaf area that we estimated by satellite remote sensing of between 5 and 6 $m^2 m^{-2}$ throughout the year [63]. The soil is a shallow, stony, loamy clay developed on schists (lithic xerorthent).

The area has a Mediterranean-type climate. Rainfall occurs during autumn and winter, and ca 80 % are between September and April. Mean annual precipitation at Vailhan, 1.5 km south of the study site, is 755 mm recorded over the previous 15 years. Mean monthly temperatures at Bédarieux 10 km north (1951–1994 period, elevation 195 m) range from 5.7 °C in January to 21.9 °C in July with a mean annual value of 13.2 °C. Penman estimates of potential evapotranspiration (PET) range between 920 and 1020 mm ha^{-1}.

2.2. Vegetation measurements

Dominant species are two evergreen trees, holm oak *(Quercus ilex)* and strawberry tree *(Artutus unedo),* which together make up 90 % of the total 36 $m^2 ha^{-1}$ basal area. Pubescent oak *(Quercus pubescens),* a deciduous species, is also present, but represents less than 3 % of the 8 870 stems ha^{-1}. Understorey species are mainly *Viburnum tinus* (2 650 individuals ha^{-1}) and *Erica arborea* (270 individuals ha^{-1}). Stem densities of *Q. ilex, A. unedo* and *Q. pubescens* were 5 280, 3 360 and 230 stems per hectare, respectively, and the corresponding mean diameters at breast height (DBH) were 7.0 ± 2.9, 6.7 ± 2.5 and 13.8 ± 4.8 cm (see *table I*). The corresponding numbers of stems per stool are 2.2 ± 0.9, 3.0 ±1.2 and 1.7 ± 1.0, respectively. New leaves of the deciduous *Q. pubescens* grew at the end of March and senesced during October. We consider the April–October period as the only active transpiration period for this species.

Estimates of leaf area index *(L)* were made in the same plot using a LAI-2000 plant canopy analyser (LI-Cor Inc., Lincoln, NE, USA). This instrument measures the gap fraction of the canopy based on diffuse blue light attenuation at five zenith angles simultaneously. Measurements were made at the nodes of a 6 × 6 grid within a 30 × 30 m area. Reference reading of sky brightness could be

Table I. Frequency distribution of tree diameters at breast height (trees ha^{-1}) in a 900 m^2 mixed Mediterranean woodland plot. Numbers in brackets indicate the number of tree on which sap flow measurements have been made.

Diameter (cm)	*Quercus ilex*	*Arbutus unedo*	*Quercus pubescens*
0–4	210	100	8
4–8	2 640	1 850 (1)	13
8–12	1 850 (4)	1 210 (2)	21
12–16	580 (1)	200 (1)	77 (1)
16–20			89
> 20			22
Total	5 280 (5)	3 360 (4)	230 (1)

obtained quickly at the top of the tower. Because direct sunlight on the canopy causes errors exceeding 30 % in the LAI-2000 measurements, we collected data only on cloudy days. LAI maps for the plot have been obtained by punctual kriging, as in Joffre et al. [34], using the SURFER package [35]. Measurements were repeated in October 1993, March 1994 and August 1994.

2.3. Meteorological data

A Campbell Scientific weather station was installed at the top of a 12 m scaffolding tower, 2 m above the top of the forest canopy. Data were stored on a CR21X datalogger. Throughout the investigation period, the system logged 30 min mean air temperature and relative humidity measured with a MP100 Rotronic probe (platinium resistance thermometer and polymer humidity sensors) inside a model 41004-5 Gill radiation shield. Auxiliary meteorological measurements included solar radiation (silicon cell pyranometer SKS1110 Skye Inst. Ltd), 30 min rainfall intensities (tipping bucket rain gauge ARG 100 calibrated for a 0.2 mm tip) and horizontal wind speed (cup

anemometer with photochopper output A100R).

2.4. Sap flow measurement

We used simple radial sap flow sensors applicable to trees [21–23]. A pair of 2 cm long probes separated vertically by 10–15 cm are implanted in the sap wood. The top probe is heated with constant power and the temperature difference between the probes monitored. The probes were installed in freshly bored holes in the outermost 2 cm of sap wood and moved every 3–4 months. The sensors were shielded from rain with a thin film of plastic and the stem was thermally insulated with 6 cm polystyrene sheet extending approximately 0.25 m above and below the sensors. The sensors were connected to a CR21X datalogger. The data logger scanned the probe signals every 1 min and recorded half-hourly means after converting probe voltage to °C. Ten trees located close to the meteorological tower were selected *(table I)*. Temperature difference between the two sensors is related to sap flux density (i.e. sap flow per unit of sap wood area, expressed in mm^3 mm^{-2} h^{-1}) by a relationship proposed by Granier

[21] and that we applied for these tree species (see discussion in Cabibel and Do [8] and Goulden and Field [20]). These sensors average the sap flux density across a sap wood radius of 2 cm. For a given tree species, sap flow for the site was estimated by multiplying its sap flux density averaged over the sampled trees by its total sap wood area. Measurement were carried out continuously from June 1, 1993 to September 30, 1994.

2.5. Ecophysiological measurements

A steady state parameter (LI 1600, LI-COR Inc., Lincoln, Nebraska, USA) was used to measure leaf stomatal conductance. Data were collected on three to five mature leaves per species chosen at random in the sunny part of the canopy from dawn to ca 2 000 hours on 7 days (18 June and 7 July 1993; 11 March, 28 April, 23 June, 4 August and 15 November 1994).

Xylem water potential (Ψ_p) was measured with a standard Scholander-type pressure chamber (PMS 1000, PMS Inst., Corvallis, Oregon, USA). A short shoot with a minimum of three leaves was cut and from which water potential was immediately measured in the field. On three trees per species, we measured two shoots per tree, if the difference between them was more than 0.2 MPa we measured a third twig.

3. ESTIMATION OF LEAF CONDUCTANCES

3.1. Theoretical background

The principles of combined energy and diffusion control have been generalised by numerous workers to produce the so-called 'combination equation', the basis for both single-layer and multilayer mod-

els for canopy evaporation [55]. This approach to simulating canopy physiology is based on the hypothesis that leaf properties can be quantitatively scaled up to canopy. As a result, with respect to energy and water flux, the canopy can be treated as a 'big-leaf'. The evaporation is then given by the Penman-Monteith [equation (1)] [44]:

$$\lambda E = \frac{\varepsilon R_n + \rho \lambda g_a D}{\varepsilon + 1 + g_a / g_c} \qquad (1)$$

where E and R_n are, respectively, the flux densities of water vapour and net irradiance per unit ground (we neglected here heat flux into the air between the trees and storage in the biomass as well as soil heat flux), D is the air saturation deficit at a reference height above the canopy, ε is the ratio of latent to sensible heat increase with temperature for saturated air, λ is the air density and λ the latent heat of vaporisation of water. Here, g_a and g_c are, respectively, the bulk aerodynamic conductance for the water vapour flux between the evaporating leaf surfaces and the reference height and the bulk canopy conductance. In our case, because of high leaf area index and leaf litter covering the soil, we neglected direct soil evaporation. The canopy conductance, g_c, can then be calculated from the inversion of equation (1):

$$g_c = \frac{\lambda E\, g_a}{\varepsilon R_n - \lambda E \left(1 + \varepsilon \right) + \rho \lambda g_a D} \qquad (2)$$

In our case, R_n was assumed to be linearly related to incoming solar radiation R_g with an absorption coefficient of 0.8 and a constant net loss of thermal radiation of 50 W m^{-2} (data not shown) was calculated using equation (3) with z_0 and d being assumed to be proportional to the stand height h and arbitrarily chosen as $d = 0.75h$ and $z_0 = 0.1h$ ([68]; see also Rambal et al. [54]):

$$g_a = \frac{k^2 u}{\ln^2\left[(z-d)/z_0\right]} \qquad (3)$$

where z_0 is the surface roughness, d is the zero plane displacement, k is the von Karman's constant and u is the wind speed at height z. To take into account the lag between E and the sap flux F we assume the damping effect due to stem storage to be represented by a linear differential equation analogue to a resistance-capacitance network [70]:

$$k_d \, dF/dt + F = E \qquad (4)$$

Solving equation (4) yields a numerical filter [equation (5)] that gives E at time t function of F in the same time interval and of F in the previous time interval

$$
\begin{aligned}
E_t &= (F_t - c_1 F_{t-1})/c_2 \\
&\text{with } c_1 = \exp(-1/k_d) \qquad (5) \\
&\text{and } c_2 = 1 - c_1
\end{aligned}
$$

The parameter k_d is adjusted by trial and error particularly at dusk when xylem sap continues to flow after stomatal closure when $E = 0$. We retained a time constant for water transport k_d of 1 500 s close to those already reported in the literature [48, 70].

Canopy stomatal conductance can be down scaled to the leaf level using methods developed for similar scaling of carbon assimilation [31, 38]. For canopies with a spherical leaf angle distribution (see discussion of this assumption in Rambal et al. [54]), the sunlit leaf area index L^* is:

$$L^* = 2 \cos \theta [1 - \exp(-0.5L / \cos \theta)] \qquad (6)$$

where θ is the zenith angle of the sun and L the leaf area index.

With estimates of canopy conductance g_c and L^*, averaged stomatal conductance g_{sw} was calculated for the three dominant already mentioned tree species as:

$$g_{sw} = g_c/L^* \qquad (7)$$

We fit stomatal conductances g_{sw} with the following multiple-constraint function [72]:

$$g_{sw} = g_{swmax} \, f_1(R_g) \, f_2(D) \, f_3(\Psi_p) \qquad (8)$$

These response functions have been successfully incorporated into semi-empirical models. The functions f_i, ranging between 0 and 1, account for the constraints on g_{sw} imposed by light, air saturation deficit D and plant water status through Ψ_p. R_g is used here as a surrogate for photosynthetically active radiation, the dominant regulator of stomatal opening. It is usually considered that stomatal conductance shows a hyperbolic response to R_g, so:

$$f_1(R_g) = 1 - \exp(R_g/k_a) \qquad (9)$$

The stomatal response to air humidity could be linear or curvilinear depending on the control system involved, a direct feedforward response results in a linear relationship, whereas a feedback response via plant water status leads to a non-linear relationship [18]. We used here a two-parameter linear feedforward relationship of the form:

$$
\begin{aligned}
f_2(D) &= 1 \\
f_2(D) &= 1 - k_c(D - k_b) \text{ for } D \geq k_b \qquad (10)
\end{aligned}
$$

3.2. Calibration of the leaf conductance model

The parameters that describe stomatal opening in response to the dependent variables were estimated by non-linear least squares regression using Marquardt's method (see limitation of this approach in Jarvis [32]). Estimations of g_{sw} were arbitrarily shared in two data sets, the 1993 period is used for calibration of the parameters and the 1994 period reserved for validation of the model. Specifically, these

two sets were split into subsets based on predawn potential classes of 0.25 MPa wide. For each subset we estimated k_b and g_{swmax} $f_3(\Psi_p)$ that we assumed to be related to Ψ_p and k_a and k_c assumed to be independent of Ψ_p.

4. RESULTS

During the 2 years of measurements, Ψ_p did not reach very negative values (*figure 1*). In 1993, *A. unedo* was the species that had the lowest Ψ_p, -1.72 ± 0.22 (SD) MPa on 15 September (day of year, DOY

258). The potentials for *Q. ilex* and *Q. pubescens* on the same day reached -1.66 ± 0.14 and -1.6 ± 0.10 MPa, respectively. In 1994, the summer drought did not have the same intensity because of the rainfall in July (17.6 mm on DOY 209 more than 24.4 mm on DOY 212). As a result, the minimum values reached on 21 September (DOY 263) were only -1.28 ± 0.04, -1.09 ± 0.19 and -0.95 ± 0.03 MPa for *A. unedo, Q. ilex* and *Q. pubescens,* respectively. Outside the summer drought period and in the absence of any water stress, Ψ_p was between -0.2 and -0.35 MPa in all three species.
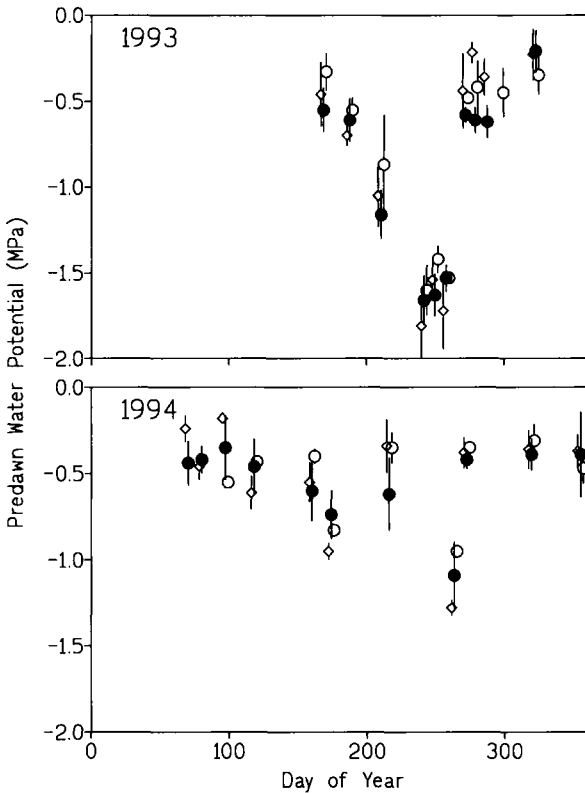

Figure 1. Time evolution of predawn water potentials for 1993 and 1994 for *Q. ilex* (filled circle plus standard deviation SD), *A. unedo* (unfilled diamond plus SD) and *Q. pubescens* (unfilled circle plus SD).

A comparison was made between the mean daily sap flow densities of each of the tree species, between April and October 1994, a period chosen to take into account the deciduous nature of $Q.$ *pubescens*. The mean flows were 3.67 ± 0.36 dm^3 d^{-1} for $Q.$ *ilex* and 2.10 ± 0.36 dm^3 d^{-1} for $A.$ *unedo*. The corresponding coefficients of variation were 10 and 17 %. The mean flow for the single individual of $Q.$ *pubescens* sampled was 2.7 dm^3 d^{-1}. Furthermore no significant relation was observed between the mean sap flow density and DBH ($r = -0.44$ ns and $r = 0.62$ ns for $Q.$ *ilex* and $A.$ *unedo*, respectively).

The area-averaged leaf area indices of the study site were 5.51 ± 0.64 in October 1993, 5.16 ± 0.65 in March 1994 and 5.60 ± 0.44 in August 1994. The combined analysis of maps of leaf area indices (data not shown) and the position of the individuals sampled showed that there was little or no overlap between crowns. The functioning of each species could therefore be considered to be separate. The overall functioning of the ecosystem would therefore be the linear combination of each of its three compartments. The analyses that follow concern the stomatal functioning analysed species by species.

The values of the parameters identified for each Ψ_p class and for each species are shown in *table II*. k_a values thus identified were 116, 132 and 100 W m^{-2} for $Q.$ *ilex*, $A.$ *unedo* and $Q.$ *pubescens*, respectively. g_{swmax} values that were reached in the absence of water stress, i.e. when Ψ_p was close to zero, were 0.9, 0.65 and 0.5 cm s^{-1}, respectively, for the same species. The relations between g_{swmax} and Ψ_p, fixed at the median value for each class, could be fitted to hyperbolic curves. These relationships were fitted to equations of the form $g_{swmax} = (a + b\Psi_p)^{-1}$ where g_{swmax} was expressed in cm s^{-1} and Ψ_p in MPa. We obtained $g_{swmax} = (0.77 - 2.35\Psi_p)^{-1}$ with $r^2 = 0.942$ ($P < 0.001$) for Q *ilex* (fig-

ure 2a), $g_{swmax} = (1.09 - 3.25\Psi_p)^{-1}$ with $r^2 = 0.985$ ($P < 0.001$) for $A.$ *unedo* (figure 2b) and $g_{swmax} = (1.67 - 2.90\Psi_p)^{-1}$ with $r^2 = 0.983$ ($P < 0.001$) for $Q.$ *pubescens* (figure 2c). The decreases in maximum conductance for the three species were significantly described by these reciprocal functions. The relationships between the parameter k_b [see equation (10)] and Ψ_p were of a sigmoid nature. These relationships were fitted to equations of the form $k_b = a / (1 + b \exp(c \Psi_p))$ where k_b was expressed in kPa and Ψ_p in MPa. We obtained $k_b = 1.77 / (1 + 29.6 \exp(5.14 \Psi_p)$ with $r^2 = 0.969$ ($P < 0.001$) for *Quercus ilex (figure 3a)*, $k_b = 1.9 / (1 + 21.8 \exp(3.59 \Psi_p)$ with $r^2 = 0.971$ ($P < 0.001$) for *Arbutus unedo (figure 3c)* and $k_b = 1.82 / (1 + 8.91 \exp(3.84 \Psi_p)$ with $r^2 = 0.944$ ($P < 0.001$) for *Quercus pubescens (figure 3c)*.

For validation, we used data from 1 January to 30 September 1994. Comparisons were made for: 1) the measured and simulated daily time courses of canopy conductance; 2) the stomatal conductances deduced from both the canopy conductances and the area of leaf subjected to direct solar radiation and to porometer measurements of leaf conductance; and 3) the measured and simulated daily transpirations for the three species taken into account and their cumulative, that is ecosystem transpiration. The simulation of the canopy conductances gave satisfactory results. The example of three consecutive days for the $Q.$ *ilex* component of the ecosystem is shown in *figure 4*. The same was true when the simulated stomatal conductances were compared with those obtained independently by porometry *(figure 5)*. The measured and simulated daily transpirations were compared for $Q.$ *ilex (figure 6a)*, $A.$ *unedo (figure 6b)* and the ecosystem *(figure 6c)*. The results for $Q.$ *pubescens* are not shown because its contribution to the total was low. At this daily scale the correlation coefficients

between the measured and simulated values were 0.83, 0.76, 0.94 and 0.85 for *Q. ilex, A. unedo, Q. pubescens* and the ecosystem, respectively. These values were all very highly significant ($P < 0.01$). The model did, however, underestimate the measured values at low rates, i.e. at values of less than 1 mm per day.

5. DISCUSSION

Spatial variations in daily sap flows in *A. unedo* and *Q. ilex* were similar in their amplitudes to what has been recorded in certain tropical rainforests [24]. They were also evident in ^{13}C isotope content of *Q. ilex* and *Q. pubescens* leaves collected from the site in October 1993, and therefore correlated with the intrinsic water use efficiency (see [19]). On ten individuals of each of these two species the $\delta^{13}C$ content varied from −29.1 and −24.7 ‰ in *Q. ilex* and −28.8 and −25.7 ‰ in *Q. pubescens* [14]. These ranges are much greater than those normally found within natural ecosystems, but are less than those recorded by Mooney et al. [45] and

Table II. Parameter values (+SE of the estimate) of equations (8)–(10) as fitted by least-square regression and the variance r^2 explained by the equations for the 1993 data sets and for the predawn potential classes.

Ψp class (MPa)	g_{swmax} (cm s^{-1})	k_a (W m^{-2})	k_b (kPa)	k_c (kPa$^{-1} \times 10^3$)	n	r^2
Quercus ilex						
0 to −0.25	0.90 (0.01)	116 (22)	0.10 (0.02)	260 (100)	414	0.67
−0.25 to −0.5	0.75 (0.02)	—	0.15 (0.01)	—	133	0.56
−0.5 to −0.75	0.43 (0.06)	—	1.0 (0.14)	—	730	0.89
−0.75 to −1.0	0.31 (0.07)	—	1.28 (0.18)	—	310	0.89
−1.0 to −1.25	0.24 (0.09)	—	1.5 (0.20)	—	241	0.63
−1.25 to −1.5	0.22 (0.09)	—	1.7 (0.17)	—	331	0.59
−1.5 to −1.75	0.21 (0.09)	–	1.75 (0.12)	—	384	0.67
−1.75 to −2.0	0.21 (0.01)	—	1.9 (0.17)	—	161	0.52
Arbutus unedo						
0 to −0.25	0.65 (0.03)	132 (25)	0.05 (0.002)	250 (100)	697	0.61
−0.25 to −0.5	0.48 (0.02)	—	0.01 (0.004)	—	632	0.73
−0.5 to −0.75	0.32 (0.03)	—	0.07 (0.050)	—	376	0.90
−0.75 to −1.0	0.24 (0.04)	—	1.1 (0.08)	—	268	0.91
−1.0 to −1.25	0.20 (0.05)	—	1.3 (0.09)	—	207	0.73
−1.25 to −1.5	0.18 (0.06)	—	1.5 (0.11)	—	209	0.75
−1.5 to −1.75	0.15 (0.07)	—	1.8 (0.13)	—	242	0.61
−1.75 to −2.0	0.11 (0.09)	—	1.95 (0.13)	—	182	0.48
Quercus pubescens						
0 to −0.25	0.50 (0.01)	100 (20)	0.05 (0.005)	260 (100)	285	0.77
−0.25 to −0.5	0.34 (0.01)	—	0.8 (0.004)	—	553	0.83
−0.5 to −0.75	0.28 (0.03)	—	1.0 (0.10)	—	255	0.85
−0.75 to −1.0	0.26 (0.03)	—	1.3 (0.11)	—	274	0.70
−1.0 to −1.25	0.20 (0.03)	—	1.6 (0.09)	—	205	0.75
−1.25 to −1.5	0.18 (0.03)	—	1.8 (0.12)	—	527	0.66

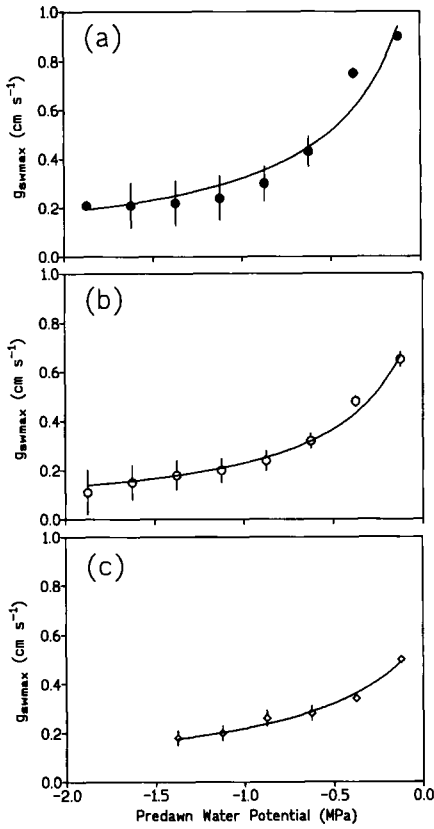n is the size of the corresponding subsample.

Figure 2. Relationships between g_{swmax} and Ψ_p for *Q. ilex* (a), *A. unedo* (b) and *Q. pubescens* (c).
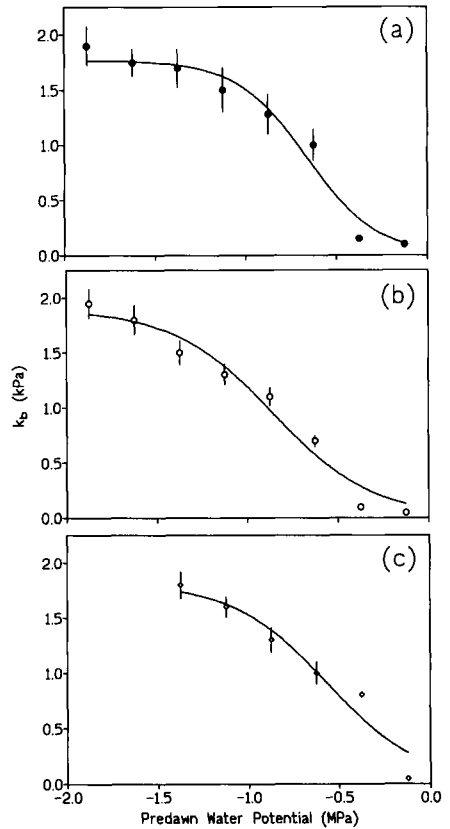
Figure 3. Relationships between k_b and Ψ_p for *Q. ilex* (a), *A. unedo* (b) and *Q. pubescens* (c).
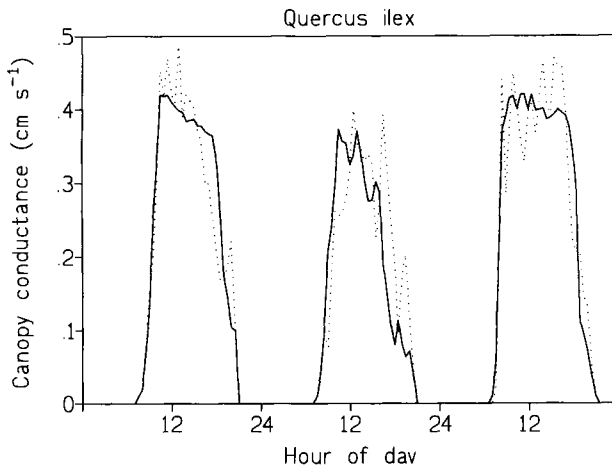

Figure 4. Comparison of diurnal evolutions of simulated canopy conductance (continuous line) with those deduced from the inversion of the Penman-Monteith equation (dotted line) for *Q. ilex* and for three consecutive days (12–14 May 1994).
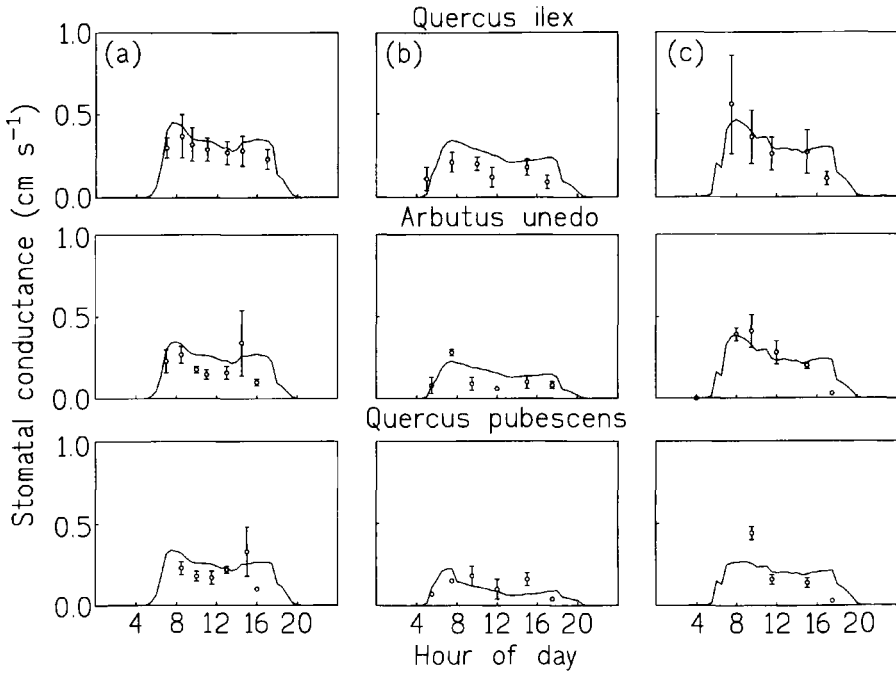
Figure 5. Comparison of diurnal evolutions of simulated stomatal conductances (continuous line) with measurements made under porometric conditions (unfilled circle plus error bars) on *Q. ilex* (a), *A. unedo* (b) and *Q. pubescens* (c) for three days (28 April, 23 June and 4 August 1994).
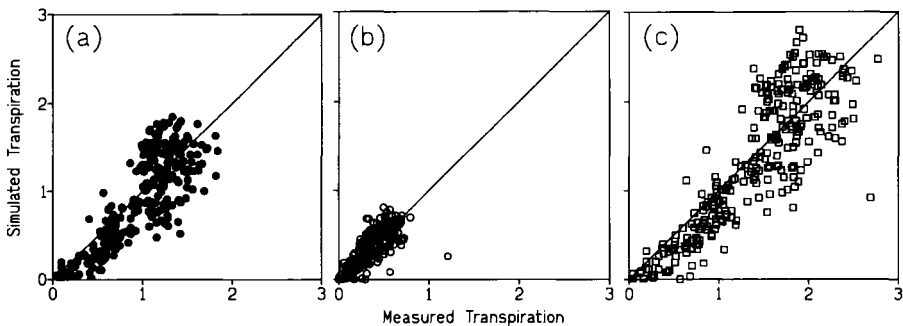

Figure 6. Comparison of simulated daily transpirations with those deduced from sap flux measurements in the validation year 1994 for *Q. ilex* (a) (filled circle), *A. unedo* (b) (unfilled circle) and for the whole ecosystem (c) (unfilled square).

Kohorn et al. [39]. The sources of variations are many. The lack of consistent trends observed for water consumption versus tree size supports the observations of Doley and Grieve [15] and Hatton and Vertessy [26]. Hatton and Vertessy [26] showed differences in daily flows that could reach 70 % between two *Pinus radiata* trees despite the fact that they were separated by only 3 m, occupied almost the same area of ground and had similar stem diameters and heights. Doley and Grieve [15] analysed differences in flows between 13 *Eucalyptus marginata* of similar size. They observed that "the water consumption could not be closely related with their diameters, heights or crown exposure although observation of the crowns suggested that the amount of leaf material may have had an important influence". This remark supports the conclusions of pioneer works of Ladefoged [41]. He found that crown shape had a marked influence on transpiration in 39 trees in several stands within mixed deciduous forests in northern Europe dominated by *Quercus petraea, Fagus silvatica* and *Fraxinus excelsior.* This remark also corroborates the recent results of Le Goff et al. [43] and Sala et al. [60] who found an almost linear relation between the leaf area of an individual tree and its cumulative water consumption in dense stands of *Fraxinus excelsior* and of salt cedar, respectively. Le Goff et al. [43] also demonstrated the importance of the social position of the tree. The importance of this social position has also been stressed by Kelliher et al. [36] in explaining variations in water consumption within a broadleaf forest of *Nothofagus* spp. The demonstration of the existence of these variations does not however call into question the work we conducted on averaged flows of individual species and for the whole ecosystem.

Inversion of the Penman-Monteith equation resulted in the case of the domi-nant *Q. ilex* in a seasonal pattern of canopy conductance *(figure 4)* which varied between 4.0 and 2.0 cm s^{-1}. This is of the same order of magnitude as that measured by Valentini et al. [71] over a Mediter-ranean macchia canopy dominated by *Q. ilex* (3.3 cm s^{-1}) and is in agreement with those proposed in the reviews of Kelliher et al. [37] and of Schulze et al. [61] for the superclasses temperate deciduous forest (2.07 $\pm$ 0.65 cm s^{-1}) and sclerophyllous shrubland (2.2 $\pm$ 0.2 cm s^{-1}). It is however greater than that of the super-class temperate evergreen broadleaf for-est which was based on only a single value, 1.4 cm s^{-1}.

The low amplitude of Ψ_p made it impossible to analyse the mechanism by which transpiration is regulated over the entire range of functioning in each of the three species studied. The analysis concerned a range of Ψ_p over which the transpiration rate remained relatively high. For example on 25 August 1994, in a neighbouring study site, Damesin and Rambal [12] recorded mean values of Ψ_p that reached -2.7 and -3.5 MPa for *Q. pubescens* and *Q. ilex.* The latter value is slightly lower than the empirical limit of -3.4 MPa found in the review made on Mediterranean evergreen oaks by Ram-bal and Debussche [50]. As for *Arbutus unedo*, it seems probable that its root system is superficial in nature, since it not only experienced the lowest Ψ_p but also showed a sharp rise in Ψ_p following the rainfall events in July 1994. Beyschlag et al. [4] measured a leaf water potential of -5 MPa in *A. unedo,* whereas two co-occurring evergreen oaks did not exceed -3 MPa. The comparison made by Castell et al. [9] of co-occurring deep-rooted *Q. ilex* compared to shallow-rooted *A. unedo* showed that Ψ_p were -2.5 and -3.4 MPa, respectively, at the peak of the summer drought.

In this latter study, the maximum stomatal conductances, averaged over the light

saturated phase of the day, that were reached in the absence of any drought stress were lower than 0.5 cm s^{-1} in *A. unedo* and at the same time reached 0.75 cm s^{-1} in *Q. ilex*. The same ranking of conductances was found by Tenhunen et al. [67] who compared *A. unedo* with two Mediterranean evergreen oaks *Q. suber* and *Q. coccifera*: g_{swmax} was 0.35 cm s^{-1} in the former, whereas it was between 0.75 and 1 cm s^{-1} for the two oaks. Rhizopoulou and Mitrakos [57] recorded values reaching 0.7 cm s^{-1} in *Q. ilex*, whereas Sala and Tenhunen [59] found a value of 0.65 cm s^{-1} (see also the review by Acherar and Rambal [1] in which g_{swmax} ranged between 0.7 and 1.05 cm s^{-1}). These comparisons are however of indicative value only because these studies were conducted under environmental conditions and on plant material (age of trees and leaves, nitrogen content) that differed and at leaf water potentials that were more or less close to zero.

For the species studied, the observations on daily changes in stomatal conductance *(figure 5)* showed that the patterns were similar to those proposed by Hinckley et al. [29, 30]. During the onset of drought, a decrease in maximum conductance was recorded which closely related to the predawn water potential and fitted to an inverse function. A relation of the same type was obtained by Pereira et al. [47] on *Eucalyptus globulus,* by Acherar and Rambal [1] on four Mediterranean oaks including *Q. ilex* and by Damesin [13] for *Q. ilex* and *Q. pubescens.* This decrease in maximum conductance was also observed in situ in other oak species by Reich and Hinckley [56] and in *Q. ilex* by Sala and Tenhunen [59] in two contrasting ecological situations: ridge and valley locations. However, these latter authors found that it could be described by a linear relation. Such a dissimilarity could be related to the rate at which soil moisture was depleted. Nev-

ertheless, in *Q. ilex* at Ψ_p less than –0.5 MPa, there was convergence between our observations and those in the literature. All of these response curves are shown in *figure 7a, b*. It can be seen that the evergreen oak maintained a high conductance at low Ψ_p. The same is true of other Mediterranean evergreen oaks: *Q. dumosa* had g_{smax} of 0.2 cm s^{-1} at –3.3 MPa; *Q. coccifera,* 0.375 cm s^{-1} at –3 MPa and *Q. suber,* 0.25 – 0.3 cm s^{-1} at –3 MPa [67].

The parameter k_a relative to the stomatal response to sunlight is in agreement with published values. An irradiance threshold of 200 W m^{-2} for temperate deciduous oaks was proposed by Thompson and Hinckley [69] and Simpson et al. [62]. A net irradiance greater than 75 W m^{-2} was adopted by Pitaco and Gallinaro [49] for *Q. ilex.* Lower threshold values, ranging between 70 and 200 (mol m^{-2} s^{-1} of photosynthetic active radiation, have been found in seedlings of *Q. ilex* and two Mediterranean deciduous oaks (Acherar and Rambal, unpublished data).

Tenhunen et al. [64–66] and Lange et al. [42] observed a depression in stomatal conductance at solar midday in several species of Mediterranean woody plants, particularly *Q. ilex* and *A. unedo.* This depression was considered to be a characteristic of Mediterranean species allowing them to reduce water losses when the evaporative demand is highest. It is probably controlled by the saturation vapour pressure deficit of the air. In contrast, Hinckley et al. [30] thought that it depends on a combination of several factors and especially the instantaneous water potential, whereas Correia et al. [11] suggested that it results from the inhibitory effects of intense photosynthetic radiation on the chloroplasts. The depressions at solar midday were not very pronounced in our results (see *figure 5*). This was also the case for observations made in situ on adult *Q. ilex* trees by Sala and Tenhunen [59]
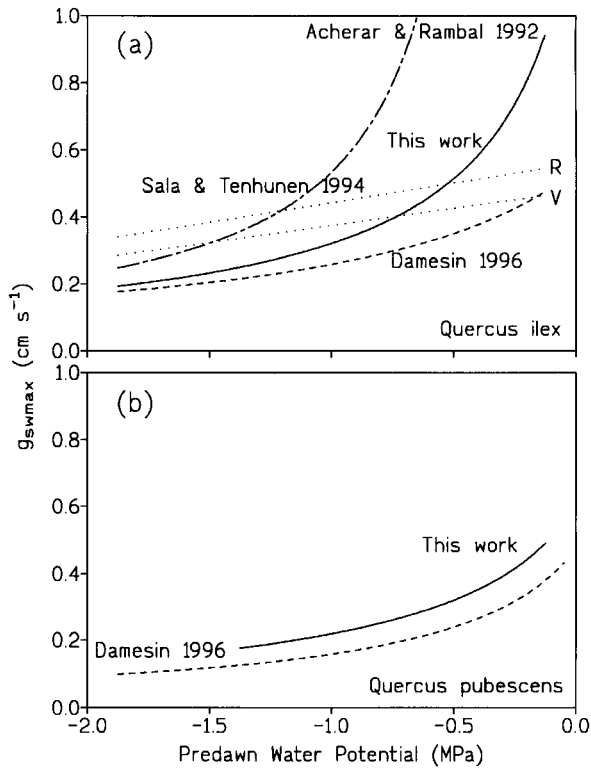
Figure 7. Comparison of the relationships between g_{swmax} and Ψ_p for *Q. ilex* (a) and *Q. pubescens* (b) with those published in some literature papers.

and on *Q. ilex* and *Q. pubescens* by Damesin [13] which also demonstrated the slight amplitude of this phenomenon. Although direct effects of air humidity surrounding leaves on stomatal aperture were limited, they do nevertheless comply with published results. The effect of *D* on stomatal opening has been demonstrated in several deciduous temperate oaks with a dg_{sw}/dD ratio ranging from −0.19 to −0.38 [7, 10, 16, 28]. That is the same order of magnitude as we recorded (0.26) in our two Mediterranean oaks. This sensitivity is much lower than that recorded by Sala and Tenhunen [59] and Pittaco and Gallinaro [49] in *Q. ilex* but similar to that observed by Hollinger [31]

in the evergreen Mediterranean oak, *Q. agrifolia* and in the deciduous, *Q. lobata*. In *A. unedo*, the response observed by Tenhunen et al. [65] indicates that the behaviour of *A. unedo* is similar to that of *Q. coccifera*. A clear midday stomatal closure occurred although it was more pronounced than that observed in *Quercus*. In *A. unedo* subjected to a water potential of between −2 and −2.5 MPa, Beyschlag et al. [4] found a sensitivity of stomatal conductance dg_{sw}/dD close to −0.2, i.e. a value similar to that of our observations.

The approach we used enabled us to take into account the functional relationships controlling stomatal behaviour and to

interpret parameters in a physical sense, even for a heterogeneous multi-species ecosystem. As stated by Jarvis [32], such a model is not truly mechanistic because it does not link environmental factors with stomatal functioning at the biochemical level. Nevertheless, its semi-empirical character makes it useful for the interpretation of field observations and prediction of both stomatal and canopy conductances. On the whole, and in spite of the simplifications inherent in the big-leaf representation of the canopy, the model is useful for predicting interactions between Mediterranean mixed woodland and the environment and for interpreting H_2O exchange measurements. This model also relies on an assumption of linearity (the summation approach in Jarvis [33]) in the respective contributions of the sap flows of the dominant species in reconstituting the flow at the ecosystem scale. This assumption is a major one, but at the present time there is no other alternative. It has also been used in estimating the total amount of RUBISCO in the canopy of a mixed forest [2] and in the calculation of the latent and sensible heats at the scale of a Mediterranean landscape [52].

In conclusion, we advocate here the use of methods in which scale-down and scale-up approaches are cyclically applied and strategically designed to address practical problems [53]. Many works refer to the standard practices normally used in resolving problems of changes of scale [17]. Bottom-up and top-down approaches tend to be opposed or even exclude one another. Paraphrasing Root and Schneider [58], we characterise this work as a 'scale-down embedded in scale-up' exercise.

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