

# Drought controls over conductance and assimilation of a Mediterranean evergreen ecosystem: scaling from leaf to canopy

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## Abstract

Drought control over conductance and assimilation was assessed using eddy flux and meteorological data monitored during four summer periods from 1998 to 2001 above a closed canopy of the Mediterranean evergreen oak tree *Quercus ilex*. Additional discrete measurements of soil water content and predawn leaf water potential were used to characterize the severity of the drought.

Canopy conductance was estimated through the big-leaf approach of Penman–Monteith by inverting latent heat fluxes. The gross primary production (*GPP*) was estimated by adding ecosystem respiration to net ecosystem exchange. Ecosystem respiration was deduced from night flux when friction velocity ( $u_*$ ) was greater than  $0.35 \text{ m s}^{-1}$ . Empirical equations were identified that related maximal canopy conductance and daily ecosystem *GPP* to relative soil water content (*RWC*), the ratio of current soil water content to the field capacity, and to the predawn leaf water potential. Both variables showed a strong decline with soil *RWC* for values lower than 0.7. The sharpest decline was observed for *GPP*. The curves reached zero for *RWC* = 0.41 and 0.45 for conductance and *GPP*, respectively. When the predawn leaf water potential was used as a surrogate for soil water potential, both variables showed a hyperbolic decline with decreasing water potential.

These results were compared with already published literature values obtained at leaf level from the same tree species. Scaling up from the leaf to ecosystem highlighted the limitation of two big-leaf representations: Penman–Monteith and Sellers'  $\Pi$  factor. Neither held completely for comparing leaf and canopy fluxes. Tower measurements integrate fluxes from foliage elements clumped at several levels of organization: branch, tree, and ecosystem. The *Q. ilex* canopy exhibited non-random distribution of foliage, emphasizing the need to take into account a clumping index, the factor necessary to apply the Lambert–Beer law to natural forests.

Our results showed that drought is an important determinant in water losses and  $\text{CO}_2$  fluxes in water-limited ecosystems. In spite of the limitations inherent to the big-leaf representation of the canopy, the equations are useful for predicting the influence of environmental factors in Mediterranean woodlands and for interpreting ecosystem exchange measurements.

*Keywords:* evergreen Mediterranean ecosystem, *GPP*, *Quercus ilex*, scaling up procedures, stomatal and canopy conductances, summer drought

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## Introduction

Modelling terrestrial ecosystem functions at site, landscape, biome or larger scales demands the development of generalized representations of the most relevant biophysical and ecological processes. The links between canopy physiology, surface energy exchange, and water and carbon dioxide exchanges have been long recognized. Models explicitly include these linkages (e.g. Running & Coughlan, 1988; McMurtrie *et al.*, 1990; Aber & Federer, 1992; Amthor, 1994; Baldocchi & Harley, 1995; Baldocchi & Wilson, 2001 among a lot of others). As emphasized by Bonan (1993): 'A future challenge [...] is not to merely show that climate change affects terrestrial ecosystems, but rather to consider what level of physiological and biophysical detail is needed to accurately model climate change impact'. In such a context, fluxes of energy, water and carbon are continuously measured with half-hourly time steps in ca. 140 stations worldwide encompassing a wide range of terrestrial ecosystems and climate. Data are collected in regional networks such as CarboeuroFlux in Europe or AmeriFlux in the USA and analyzed in synthesis products within the framework of Fluxnet (Baldocchi *et al.*, 2001). Flux towers are remarkable tools for monitoring ecosystem metabolism, for supporting validation of biogeochemical models and for helping us to understand how ecosystems respond to ecological events of different intensity and duration such as droughts.

Water availability has been shown to have dominant or co-dominant effects in the productivity of most terrestrial biomes of the Earth (Churkina & Running, 1998). This is particularly true today within Mediterranean-type climate areas and will become crucial under Global Change (Mouillot *et al.*, 2002). In these areas, natural vegetation has to cope with a strong seasonality under environmental conditions where cold wet winters alternate with hot dry summers. Drought has been identified as the major factor shaping vegetation and controlling plant functions in Mediterranean-type ecosystems (Rambal, 2001). When attempting to study mass and energy exchanges or water yield from vegetation-covered watersheds, one must take into account the interactions between soil or plant status, stomatal opening and atmospheric demand. Such interactions must be considered at different scales. Scaling from leaf to canopy represents not only a change of spatial scale but also an integration of temporal scales. Scaling is used here in Norman (1992)'s sense i.e. 'scaling implies an intuitive leap that provides a quantitative connection between distant phenomena – a short cut'. Validating modelling efforts requires measurements obtained at different temporal and spatial scales.

A continuous eddy covariance measurement program associated with ancillary ecological data acquisition was conducted within an evergreen Mediterranean woodland. These data link the local-scale environmental conditions with micro-scale leaf functioning, and consequently provide the opportunity to propose and test a model of canopy physiology. In this context, big-leaf approaches such as those proposed by Monteith (1964) and Sellers *et al.* (1992) provided useful simplified descriptions and the basis to explore stomatal effects on canopy conductance and assimilation. The present study was undertaken to: (1) examine how eddy fluxes remotely sense the effects of drought on both water and CO<sub>2</sub> regulation; (2) derive canopy conductance and assimilation from eddy flux data; (3) identify and validate empirical equations constrained by plant or soil water status that may be further used in biogeochemical and dynamico-functional models for landscape or regional scales; and finally, (4) provide a new insight into the possibility to scale up canopy regulation from basic leaf-level relationships.

## Site description and methods

### Site description

The study site is located 35 km NW of Montpellier (southern France) in the Puéchabon State Forest (3°35'45"E, 43°44'29"N and elevation 270 m) on a flat plateau. This forest has been managed as a coppice for centuries and the last clear cut was performed in 1942. Vegetation is largely dominated by a dense overstorey of the evergreen tree *Quercus ilex*. The mean tree height was about 5.5 m. In 2001, the density of the resprouted stem was 7149 stems ha<sup>-1</sup>. Stems with DBH < 4 cm represent 12% of the total stems, whereas stems with DBH > 10 cm represent 12.5%. The above-ground biomass is about 11 300 ± 2800 g dry matter (DM) m<sup>-2</sup>. Understorey species compose a sparse (percent cover lower than 25) shrubby < 2 m layer with *Buxus sempervirens*, *Phyllirea latifolia*, *Pistacia terebinthus* and *Juniperus oxycedrus*. Overstorey LAI has been evaluated using an LAI 2000 Plant area meter (Li-Cor Inc., Lincoln, NE, USA) on seven randomly distributed transects (LAI = 2.9 ± 0.4, n = 81 measurement points).

The area has a Mediterranean-type climate. Rainfall occurs during autumn and winter with about 75% between September and April. The mean annual precipitation is 883 mm with a range of 550–1549 mm recorded over the previous 18 years. The mean annual temperature over the same period is 13.5°C. This forest grows on hard Jurassic limestone. Soil texture is homogeneous in the 0–50 cm layer (39.6% clay and 14.1% sand) and belongs to the silty clay loam area of

the US Department of Agriculture (USDA) texture triangle. The soil fills up the cracks and fractures and this provides a source of water throughout the long dry summers for the deep-rooted *Q. ilex*. The averaged volumetric fractional content of stones and rocks is about 0.75 for the top 0–50 cm and 0.90 for the whole profile.

#### *Flux measurement and data selection*

Carbon and water flux measurements were performed with the eddy covariance technique from an 11 m tall scaffolding tower about 5 m higher than the top of the dominant trees. The wind speed and virtual temperature were measured with a three-dimensional sonic anemometer (Solent R2 period 1998–1999 and R3 period 2000–2001, Gill Instruments, Lymington, England). Air was drawn from an inlet located 20 cm apart from the sonic anemometer-sensing path (height 12.2 m) and through an infrared gas analyzer (IRGA) (model LI 6262, Li-Cor Inc.) with an atmospheric pressure sensor. Air entering the inlet line passed through a 0.2 µm filter (PTFE Acro 50, Pall Corp., Ann Arbor, MI, USA) followed by 1.5 m of sampling PTFE tube with an inner diameter of 4.8 mm. Airflow then passed through the analyzer housed inside a plywood weatherproof box. The flow was maintained at 8 L min<sup>-1</sup> by a pump (Novair G12/8 Novair, Sevrans, France). The IRGA was operated in absolute mode with a constant slow flow (0.03 L min<sup>-1</sup>) of ultra-high purity (UHP) nitrogen passed through the reference cell. The reference gas was initially passed through soda lime and magnesium perchlorate, removing trace amounts of CO<sub>2</sub> and H<sub>2</sub>O. The IRGA is calibrated every 3 weeks for CO<sub>2</sub> by introducing reference gas (500 ppm). For water vapor concentration, the span was checked every 4–6 weeks by comparing the H<sub>2</sub>O mixing ratio measured by the IRGA with those calculated from relative humidity and temperature from a shielded MP100 Rotronic probe (Rotronic Inst. Corp., Huntington, NY, USA) at the same height as the inlet. A dew point generator (model 610, Li-Cor Inc.) was used quarterly. Signals from the sonic anemometer and raw outputs for CO<sub>2</sub>, H<sub>2</sub>O and temperature from the IRGA were transferred to a computer through the sensor input module of the anemometer and via RS485 and RS232 serial protocols. The sampling rate was 21 Hz. The raw data were stored on site by the EdisolW software and further backed up to the lab for calculations. The whole system is powered by a solar plant plus a fuel generator located 300 m apart. The exchange rates of carbon dioxide ( $F_c$ ), latent heat ( $LE$ ) and sensible heat were estimated following Aubinet *et al.* (2000). The mean and fluxes were calculated as a block average over a 30 min time period.

The data were screened to remove possible eddy covariance instrumentation problems. Data obtained during rain events, as well as those from the next day were not selected because evaporation of the intercepted water results in inaccurate estimates of canopy conductance. Assimilation data were considered only for days when cumulated incoming solar radiation exceeded 20 MJ.

#### *Ancillary data*

A Campbell Scientific weather station (Loughborough, UK) was installed at the top of the tower. The sensors were sampled every 5 min and half-hour averages were computed and stored on a CR-21 × data logger. The air temperature and relative humidity were measured with an MP100 Rotronic probe (platinum resistance thermometer and polymer humidity sensors) inside a model 41004-5 Gill radiation shield (Gill Inst. Ltd. Lymington, UK). Auxiliary meteorological measurements included solar radiation (silicon cell pyranometer SKS1110 Skye Inst. Ltd, Powys, UK), photosynthetically active photon flux density (Li 190 S Crystalline Silicon Cells, Li-Cor Inc.), net radiation balance (REBS-Q7 Net Radiometer, Campbell Sci, USA). Soil heat flux plus heat storage in the trunk G have been previously related to net radiation as a constant fraction, 0.06 (data not shown).

#### *Soil and plant water status*

Six holes were drilled to 4.7 m depth for installation of access tubes in 1984. The holes were drilled on a grid pattern at 5 m intervals with a self-propelled wagon-drill. A whole year was allowed for settling of loose materials around the tubes. Measurements were made at 20 cm intervals from 10 to 450 cm in depth using a neutron moisture gauge (DMG 11, Ronly Electronics Ltd., Rishon Lezion, Israel, neutron source 3700 MBq <sup>241</sup>Am-Be, neutron detector <sup>10</sup>B<sub>F</sub><sub>3</sub> and from July 2001 with a CPN503 Campbell Pacific (Campbell Pacific Nuclear Int., Martinez, CA, USA), neutron source 1850 MBq <sup>241</sup>Am-Be, neutron detector <sup>3</sup>He). The calibration of thermal neutron counts against soil water content was carried out by a method detailed in Rambal (1984). A hemispherical polyethylene reflector at the surface was used for measurement at 10 cm depth. These measurements were performed once a month. The soil water storage was computed by numerical integration of the profile of soil water content and then averaged from the six profiles. On the same day, xylem water potential ( $\Psi_p$ ) was measured with a standard Scholander-type pressure chamber (PMS 1000, PMS Inst., Corvallis, OR, USA) on three trees. On each tree, two shoots with a minimum of three leaves were cut

and the water potential was immediately measured. If the difference between the two shoots was more than 0.2 MPa, a third shoot was measured.

Interpolation of the soil water storage values was carried out with a soil water balance model (see detailed description in Rambal, 1993). It simulates on a daily basis the water balance components (transpiration, evaporation and deep drainage or water yield) and the water status of the rooted soil layer and of the plant canopy (predawn and minimum leaf water potentials). The evaporation component includes the evaporation from soil under the plant canopy and the evaporation of intercepted rainwater. Comparison of measured against simulated soil water storage showed very good agreement. The standard error of the estimate was lower than 7% ( $n = 35$ ) (Rambal & Hoff, 1998).

The average value of soil water content for the entire 0–450 cm profile is equal to the soil water storage divided by the depth. We used a Campbell-type equation (Campbell, 1974; Buchan & Grewal, 1990) for representing the soil moisture characteristic or retention curve linking potential and soil water content. This equation was further expressed using the relative water content (RWC), the ratio of current water content to water content at field capacity. The soil field capacity was estimated at a pressure value of –33 kPa.

#### Estimation of canopy conductance

The canopy conductance or surface conductance,  $g_{cw}$ , was calculated from the inversion of the Penman–Monteith equation (Monteith 1964):

$$g_{cw} = \frac{\lambda E g_{aw}}{\varepsilon(R_n - S) - \lambda E(1 + \varepsilon) + \rho \lambda g_{aw} D}, \quad (1)$$

where  $E$  and  $(R_n - S)$  are, respectively, the flux densities of water vapor and net irradiance per unit ground,  $R_n$ , minus heat flux into the air between the trees as well as heat flux stored in the biomass and the soil,  $S$ .  $D$  is the water vapor saturation deficit of air at the reference height above the canopy,  $\varepsilon$  is the ratio of latent to sensible heat increase with temperature for saturated air,  $\rho$  is the air density and  $\lambda$  is the latent heat of vaporization of water.  $g_{aw}$  and  $g_{cw}$  are, respectively, the bulk aerodynamic conductance for the water vapor flux between the evaporating leaf surfaces and the reference height and the bulk canopy conductance.  $g_{aw}$  is derived from sonic anemometer outputs as  $u_*^2/u$ , where  $u$  is the mean wind speed and  $u_*$  is the friction velocity;  $g_{cwmax}$  is the daily maximum of  $g_{cw}$ . We further discuss the relationships of  $g_{cwmax}$  with drought conditions.

#### Estimation of canopy GPP

In the following text, CO<sub>2</sub> flux ( $F_c$ ) is reported as positive or source if directed away from the surface. The ecosystem respiration ( $R_{eco}$ ) has been evaluated using night-time  $F_c$ . Half-hourly values of night-time  $F_c$  were considered only when  $u_* > 0.35 \text{ m s}^{-1}$ . Night  $\overline{R_{eco}}$  was next calculated as the average of the night  $F_c$  if more than five half-hourly periods filled these wind conditions.  $\overline{R_{eco}}$  for the whole day was corrected for the mean daily soil temperature assuming dependence for temperature with the model of Lloyd & Taylor (1994):

$$GPP_{\text{day}} = \sum_{\text{day}} (F_c + \alpha \overline{R_{eco}}) dt, \quad (2)$$

where  $\alpha$  is the ratio of mean 24 h- $R_{eco}$  and of night-time  $\overline{R_{eco}}$ .

#### Scaling up with the $\Pi$ factor

Canopy performance could be described as following:

Canopy performance = TOC leaf performance  $\times$   $\Pi$  factor  $\times$  environmental forcing, where  $\Pi$  is the scaling-up factor. Sellers *et al.* (1992) assumed that the leaf performances within the canopy followed the radiation-weighted time-mean  $PAR$ , whose extinction could be described by a negative exponential of the  $\bar{k}$  parameter. The  $\Pi$  factor, or canopy  $PAR$ -use parameter, was defined as the ratio of the radiation-weighted time-mean fraction of absorbed  $PAR$ ,  $\overline{f_{APAR}}$  and of  $\bar{k}$ , where  $f_{APAR} = APAR/PAR$ ,  $APAR$  being the absorbed  $PAR$ .

For canopies such as those of *Q. ilex*, the non-random distribution of foliage elements or canopy clumping is known to enhance radiation transmission throughout the canopy. To account for this effect, a Markov model (Nilson, 1971) was used to compute directional extinction coefficients. The angular dependence of the leaf dispersion parameter or clumping factor was estimated following Kucharik *et al.* (1999). The parameters of this model, as well as those of the leaf inclination distribution function, were estimated from directional gap fraction measurements from the seven LAI-2000 transects randomly distributed around the flux tower and destructive measurements of plant area index (data not shown), following methods similar to those described in Kucharik *et al.* (1999) and Nouvellon *et al.* (2000). We used a leaf scattering coefficient in the  $PAR$  domain of about 12% for *Q. ilex* leaves. The leaf growth-irradiance history was considered by integrating over both day length and the leaf expansion period that occurs between approximately DOY 120 (budburst) to 180 (unpublished data).

### Leaf properties: a literature survey

As substantial works have been already published on the ecophysiology of *Q. ilex*, we decided to use a literature survey as the source of data for evaluating the relationships between both conductance and assimilation with plant water status.

Considering leaf conductance analysis, the early morning, light-saturated stomatal conductance, further called maximal conductance,  $g_{swmax}$ , was used. It was preferred over the midday value because of the well-known midday depression occurring when soil drought and air VPD become more intense (Tenhunen *et al.*, 1981; Lange *et al.*, 1982). Most of the literature data have been obtained on mature trees growing under natural conditions. Stomatal conductance has been measured with steady-state porometers and the plant water status is always estimated with predawn leaf water potential values (Castell, 1992; Damesin *et al.*, 1998; Tognetti *et al.*, 1998; Sala, 1999). One result was obtained on saplings growing in pots under natural conditions (Acherar & Rambal, 1992). Another result was derived from canopy transpiration measured by sap flow and validated against porometer values (Teixeira Filho *et al.*, 1998).

Considering leaf GPP, we selected the daily integral. We used literature observations of the daily courses of leaf assimilation obtained with a portable chamber and photosynthesis system (Rambal, unpublished; Castell, 1992; Tretiach *et al.*, 1997; Kesselmeier *et al.*, 1998). These values were cumulated over the day and the night-time respiration component added. Respiration was calculated assuming that respiration at 20°C is equal to  $1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and that the dependence for temperature follows a  $Q_{10}=2$ -type equation within the range of observation conditions (Turnbull *et al.*, 2001).

### Results

We first analyzed the results synthesized at the leaf level. At this scale, plant water status and water limitation are characterized by the leaf predawn potential  $\Psi_p$ . In the considered studies, except Sala (1999) the one that used a straight line, the authors fitted  $g_{swmax}$  to  $\Psi_p$  using an inverse function equation (data not shown) with  $g_{swmax}$  expressed in  $\text{cm s}^{-1}$  and  $\Psi_p$  in MPa:

$$g_{swmax} = \frac{1}{(a - b\Psi_p)}. \quad (3)$$

Between-study variations are rather large when  $\Psi_p$  values are greater than  $-1$  MPa (Fig. 1), but estimates converge for lower predawn potential values. The dependence of leaf  $GPP_{day}$  on  $\Psi_p$  derived from the literature values showed lower between-study varia-

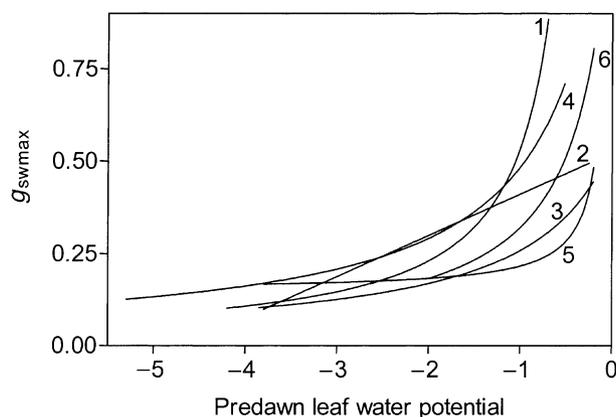


Fig. 1 Literature survey of relationships between maximal leaf conductance  $g_{swmax}$  ( $\text{cm s}^{-1}$ ) and predawn leaf water potential  $\Psi_p$  (MPa) for *Quercus ilex* leaves: 1 Acherar & Rambal (1992), 2 Sala & Tenhunen (1994), 3 Damesin *et al.* (1998), 4 Tognetti *et al.* (1998), 5 Castell (1992), 6 Teixeira Filho *et al.* (1998).

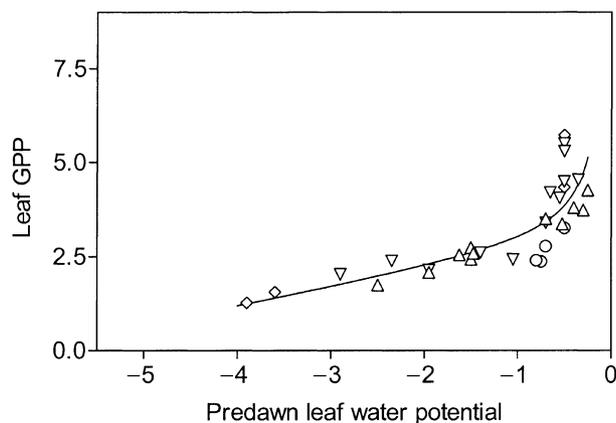


Fig. 2 Literature survey of relationships between daily leaf GPP ( $\text{g C m}^{-2}$ ) and leaf water potential  $\Psi_p$  (MPa) for *Quercus ilex* leaves. Up triangle (Castell, 1992), down triangle (Rambal, unpublished), diamond (Tretiach *et al.*, 1997), open circle (Kesselmeier *et al.*, 1998).

tion than those observed for  $g_{swmax}$  (Fig. 2). This dependence has been adjusted to a linear decline plus a hyperbolic decline describing the strong sensitivity of assimilation to values of  $\Psi_p$  close to zero:

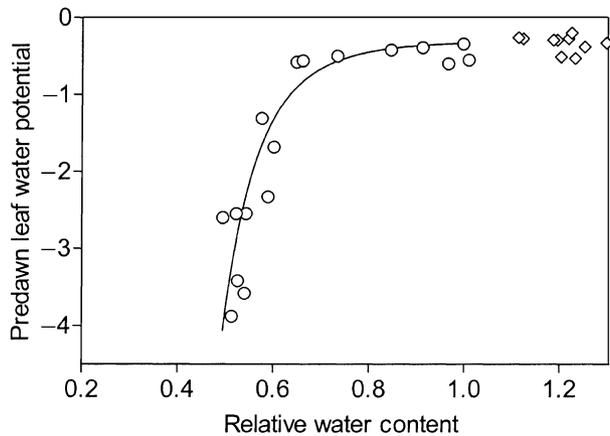
$$GPP_{day} = \frac{a}{\Psi_p} + (b\Psi_p + c). \quad (4)$$

Leaf  $GPP_{day}$  was expressed in  $\text{g C m}^{-2}$  and  $a = -0.58$ ,  $b = 0.47$  and  $c = 2.92$  ( $r^2 = 0.70$ ;  $n = 28$  and  $s_{yx} = 0.66$ ). Both equations were further used as reference equations in analyzing the ecosystem responses.

At the ecosystem scale, the available eddy flux data were as follows: (1) from July 3 to September 30, 1998, (2) from June 5 to September 15, 1999, (3) from July 28 to

**Table 1** Rainfall characteristics within the 4 measurement years. We also reported the severity of the plant–water stress, evaluated with the minimal predawn potential observed within summer, and its date of occurrence

	1998	1999	2000	2001
Annual rainfall (mm)	550	1102	756	818
May–August rainfall (mm)	101	329	231	176
Minimal $\Psi_p$ (MPa)	$-4.26 \pm 0.26$	$-1.93 \pm 0.12$	$-3.00 \pm 0.17$	$-4.13 \pm 0.18$
Date of occurrence	September 01	July 23	September 19	August 14

**Fig. 3** Relationship between predawn leaf water potential  $\Psi_p$  (MPa) and relative water content (RWC) measured the same day over 450 cm soil depth (open circle). A power function was fitted with an exponent parameter close to values predicted by pedotransfer functions driven by texture. The predawn values observed when the soil has not yet fully drained (wet soil  $RWC > 1$ ) are shown by diamonds and have not been considered in our analysis.

September 28, 2000, and (4) from April 13 to October 3, 2001. The 4 years showed contrasted length and intensity of summer droughts (see Table 1). The amount of rainfall during the summer months (May–August) was a good descriptor of the drought intensity.

The relationship between  $\Psi_p$  and relative water content RWC has been fitted to an equation of the form (Fig. 3):

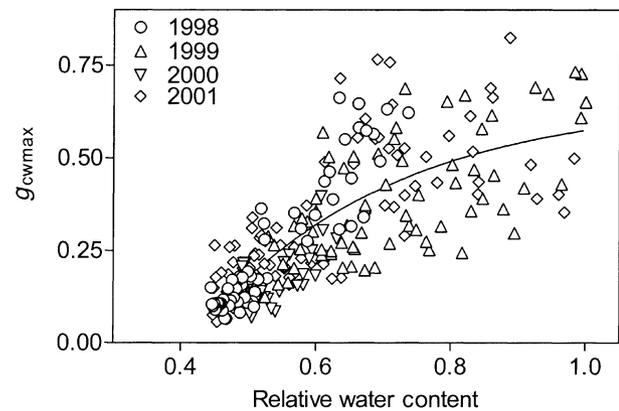
$$\psi_p = \psi_0 RWC^b + \psi_{p0} \quad (5)$$

for RWC values lower than 1, i.e. for well-drained soil conditions. The estimated parameters are  $\psi_0 = -0.033$  MPa,  $b = -6.73$  and  $\psi_{p0} = -0.30$  MPa ( $r^2 = 0.77$ ;  $n = 23$  and  $s_{yx} = 0.61$ ). This equation is subsequently applied to render a continuous estimate of  $\Psi_p$  along the four study periods.

The relation between  $g_{cwmax}$  and RWC was fitted to a one-phase exponential association (see Fig. 4):

$$g_{cwmax} = a(1 - e^{-b(RWC - RWC_0)}), \quad (6)$$

where  $g_{cwmax}$  was expressed in  $cm s^{-1}$  with  $a = 0.66$ ,  $b = 3.57$  and  $RWC_0 = 0.41$  ( $r^2 = 0.63$ ;  $n = 253$  and

**Fig. 4** Relationships between maximal canopy conductance  $g_{cwmax}$  ( $g C m^{-2}$ ) and relative water content RWC for the four summer drought periods 1998–2001. Open circles correspond to 1998, up triangle to 1999, down triangle to 2000 and diamond to 2001.

$s_{yx} = 0.11 cm s^{-1}$ ). The relations between  $g_{cwmax}$  and  $\Psi_p$  could be derived by combining Eqns (5) and (6), and is depicted in Fig. 5 as a fine line. An alternative equation has been fitted using Eqn (3) as for the leaf. We obtained  $a = 1.33$  and  $b = 1.77$ . The decline in maximum conductance according to  $\Psi_p$  was significantly described by this inverse function in accordance with most studies ( $r^2 = 0.64$ ,  $n = 253$  and  $s_{yx} = 0.109 cm s^{-1}$ ) (Fig. 5).

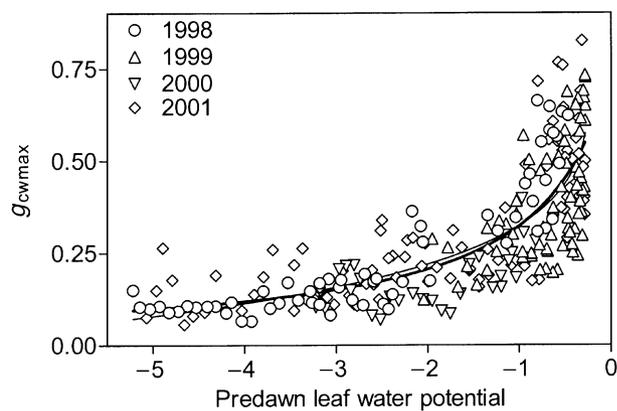
The relation between ecosystem  $GPP_{day}$  and RWC of soil (Fig. 6) was of one-phase exponential association too:

$$GPP_{day} = a(1 - e^{-b(RWC - RWC_0)}), \quad (7)$$

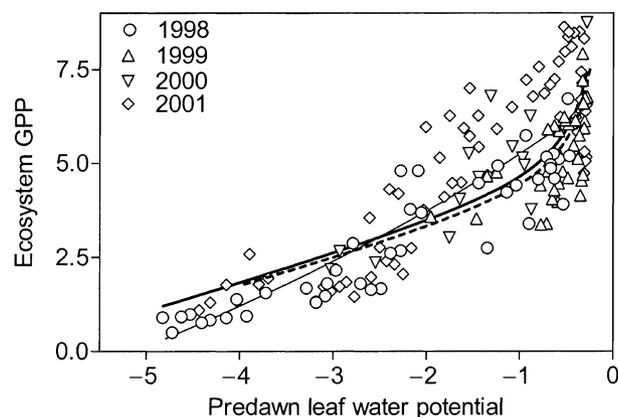
where ecosystem  $GPP_{day}$  was expressed in  $g C m^{-2}$  with  $a = 6.41$ ,  $b = 10.88$  and  $RWC_0 = 0.45$  ( $r^2 = 0.71$ ;  $n = 158$  and  $s_{yx} = 1.15$ ). The relations between ecosystem  $GPP_{day}$  and  $\Psi_p$  could be derived by combining Eqns (5) and (7) (fine line in Fig. 7). The relationship between ecosystem  $GPP_{day}$  and leaf  $GPP_{day}$  derived from Eqn (4) was (bold line on Fig. 7)

$$GPP_{day} = 1.53 leaf GPP_{day} \quad (8)$$

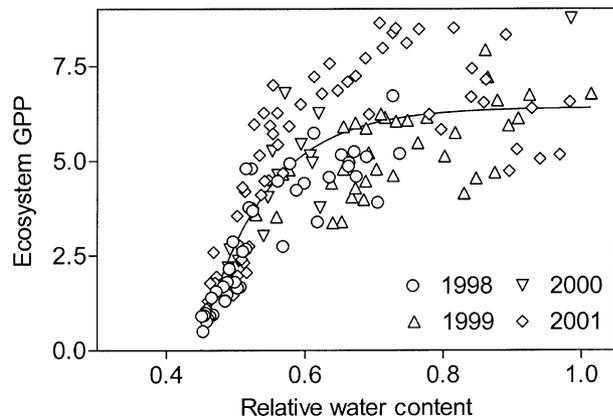
with  $r^2 = 0.66$ ;  $n = 158$  and  $s_{yx} = 1.24$ .



**Fig. 5** Relationships between maximal canopy conductance  $g_{cwmax}$  ( $gCm^{-2}$ ) and predawn leaf water potential  $\Psi_p$  (MPa). The fine line has been obtained by combining Eqns (5) and (6) (see text). The bold line has been fitted with the inverse function Eqn (3). Symbols as in Fig. 4.



**Fig. 7** Comparison of the relationships between daily ecosystem  $GPP$  ( $gCm^{-2}$ ) and  $\Psi_p$  (MPa). The fine line has been obtained by combining Eqns (5) and (7). The dashed line corresponds to ecosystem  $GPP$  values scaled up from leaf  $GPP$  using the  $\Pi$  factor approach (see text). The bold line has been obtained using ecosystem  $GPP$  values through Eqn (8).



**Fig. 6** Relationships between daily ecosystem  $GPP$  ( $gCm^{-2}$ ) and relative water content  $RWC$ . Symbols as in Fig. 4.

## Discussion

### Soil and plant water status

One of the objectives of this work was to find what state variable might be chosen for characterizing water limitation. Abundant literature for ecosystems growing under water-limited conditions, such as those in the MT climate, has focused on the key role of air  $VPD$  alone. The authors generally assumed a co-variation of  $VPD$  and soil drought (Law *et al.*, 2001). From a simulation model perspective, the easiest variable to use is the soil water stored over the root zone or derived variables such as  $RWC$ , relative extractable water content ( $REW$ ) or even a water stress index (Baldocchi, 1997; Granier *et al.*, 2000). The main limitation in using  $REW$  is the

definition of the lower limit in soil water content that is species dependent. In the case of the deep-rooted tree species, it is difficult to measure accurately as to how much water is stored in the whole profile and available for the plant (see Rambal, 1984). In the case of *Q. ilex*, we observed root water extraction at more than 4 m depth (data not shown). Unfortunately, most of the published works used top soil water as an index for the whole profile even if the species studied were deep-rooted ones (Arneeth *et al.*, 1998a). Graysson *et al.* (1997) warned against the abuse of single wetness index and suggested the development of distinct indices for wet and dry states as well as a switching criterion.

Actually, the availability of the soil water for the plant depends on its energy status (see Cochard *et al.* (2002) for a substantial account). Soil water content and soil water potential are related by the so-called retention curve, whose parameters are strongly dependent on soil texture (Campbell, 1985). The prediction of such parameters by pedotransfer functions is an imperfect exercise and this accuracy is lowered in fine-textured soil (Kern, 1995). Predawn leaf water potential is often used as a surrogate for soil water potential based on the expectation that predawn  $\psi$ ,  $\psi_p$ , is in equilibrium with the 'wettest' soil layer  $\psi$  accessed by the roots. This confers a great advantage to the use of  $\psi$  after a rain event in summer. The top-soil moisture is close to field capacity, the whole soil storage is slightly modified and both plant potential and stomatal opening show significant changes. Even if some disequilibrium between soil and plant predawn  $\psi$  may be observed (Donovan *et al.*, 2001), plant potential offers the best tool to describe soil and plant water limitation under field

conditions. Most of the leaf ecophysiology works in the literature used  $\psi_p$  to quantify the drought. In our case, the derivation of the retention function yields good results. We found a similarity between the exponent derived from predawn values and soil *RWC* ( $b = -6.73$ ) with results derived from pedotransfer functions. Using Saxton *et al.*'s (1986) equation yields  $-6.89$ . The large analysis of Clapp & Hornberger (1978) showed an averaged value of  $-7.75$  for silty clay loam soil. The simpler model of Cosby *et al.* (1984) tends to overestimate with a value of  $-9.31$ . The disequilibrium  $\psi_{p0}$  is of 0.3 MPa, a value ranging in the lowest class of the Donovan *et al.* (2001)'s analysis.

#### Scaling up with the $\Pi$ factor

Under well-watered conditions, ecosystem  $GPP_{day}$  averaged  $6.9 \text{ g C m}^{-2}$ , but ranged between 4.7 and  $8.8 \text{ g C m}^{-2}$ . These values agree with the simulations carried out by Hoff *et al.* (2002), which ran Forest-BGC on the same site. Most of the variation of  $GPP_{day}$  that we observed may be explained by temperature rather than solar irradiance. For  $RWC > 0.7$ , the relationship of  $GPP_{day}$  with the daily mean air temperature follows a bell-shaped curve that we approximated by a quadratic equation with maximum  $GPP_{day} = 7.8 \text{ g C m}^{-2}$  at  $15.7^\circ\text{C}$  ( $r^2 = 0.60$ ;  $n = 28$  and  $s_{yx} = 0.87 \text{ g C m}^{-2}$ ). Our  $GPP_{day}$  are slightly lower than those observed in some needle-leaved evergreen forests with a large range of *LAI*:  $7.5 \text{ g C m}^{-2}$  for a *Pinus ponderosa* open forest in Central Oregon (Anthoni *et al.*, 1999),  $9.6 \text{ g C m}^{-2}$  for dense *Pinus radiata* plantation (Arneeth *et al.*, 1998b) and  $9.6 \text{ g C m}^{-2}$  too for a *Pinus pinaster* forest with moderate *LAI* (Berbigier *et al.*, 2001).

Since the pioneer simulation exercises with biogeochemical models of Eckardt *et al.* (1975) and Miller *et al.* (1978) carried out in Mediterranean-type ecosystems, most models derive canopy performance from that of the leaf. Among these, Sellers *et al.* (1992) provide a good conceptual framework and has the merit of breaking the procedure down into stages. It may scale up from top-of-the-canopy (*TOC*) leaf performance to whole-canopy performance and provide good estimates of the area integrals of photosynthesis, even for spatially heterogeneous vegetation cover.

We obtained a  $\bar{k}$  value of 0.59, which is close to the estimates of Caldwell *et al.* (1986), derived from *PAR* measurements above and within *Q. coccifera* shrublands canopies. They found an extinction coefficient of 0.60. A value of 1.46 was obtained for the  $\Pi$  factor, very close to the empirical value of 1.53 (Eqn (8)). Using the  $\Pi$  factor approach to scale up canopy  $GPP_{day}$  from the *TOC leaf*  $GPP_{day}$  based on  $\psi_p$  yielded an upscale curve shown in Fig. 7 (dashed line). The values of ecosystem

$GPP_{day}$  derived from this curve are very close – although slightly lower – to the observed values or to the values obtained from the models fitted on the cloud of data (bold line). These results therefore demonstrate the usefulness of such a simple approach for producing reasonable estimates of canopy photosynthesis, from information on soil water status and *TOC leaf* performance. We may observe, however, that model accuracy is strongly dependent on accurate estimation of the  $\bar{k}$  parameter, which in turn depends on a realistic description of the canopy structure. Although non-random distribution of foliage elements is a feature shared by most forest ecosystems, its effects on directional light extinction coefficient and  $\bar{k}$  parameter is generally poorly known and often ignored. In the case of our *Q. ilex* canopy, assuming a random distribution of foliage elements yields a  $\bar{k}$  value of 0.82 (clumping factor = 0.72), a  $\Pi$  factor of 1.14 and canopy  $GPP$  values 21% lower than those obtained when the clumping of the canopy is not ignored. These results are in agreement with the findings of previous studies. Sala (1999) compared simulation results obtained with a multilayered model for a *Q. ilex* canopy with leaves randomly arranged, and for a canopy with clustered leaves in the top layer with a clumping factor of 0.8. Yearly assimilation for an *LAI* = 3 was 15% higher in the clustered version. For water, the effect is lower than 10%, so the water use efficiency is improved by only 5%. Wang & Polglase (1995) showed how canopies with high *LAI* such as those of humid tropical forests decrease the net primary production as their clumping factor changed from 0.7 towards 1. The net primary production decreases by up to 10%. These changes are higher in the deciduous forest where Baldocchi & Wilson (2001) worked. Comparing a clumping factor of 0.84 or ignoring clumping yielded net ecosystem exchange of  $-527$  and  $-309 \text{ g C m}^{-2}$ , respectively, for high *LAI*. They observed an amplifying effect from scale ranging from hour to year in their computations. At lower *LAI*, the role of the clumping decline: 15% for net ecosystem exchange, 10% for canopy photosynthesis and only  $> 5\%$  for evaporation. These values are in agreement with Sala's (1999) findings and show that, at low *LAI*, the discrepancies are in the same order as those obtained with boreal ecosystems by Wang & Polglase (1995).

Another potential source of errors in the Sellers *et al.* (1992) approach arises from their assumption that the actual profile of leaf properties follows the optimal profile, which is known to be inaccurate for most canopies. In *Q. ilex* canopies, the observed extinction coefficients of exponential curves describing the changes of leaf *N* or *LMA* with depth or leaf area index are less than optimum (Rambal *et al.*, 1996). Such

differences are known to occur rather widely, irrespective of the nature of the species (Anten, 1997; Anten *et al.*, 1995). We have compared the extinction coefficients for leaf  $N$ ,  $k_N$ , and for  $LMA$ ,  $k_{LMA}$ , with the extinction of the radiation-weighted time-mean  $PAR$ ,  $\bar{k}$ .  $\bar{k}$  is far higher than the coefficient observed for  $k_N$ , and  $k_{LMA}$ , 0.222 (Rambal *et al.*, 1996). The site-specific nature of the extinction parameter for woodlands growing around the Mediterranean basin (see Rambal, 2001) is in agreement with dePury & Farquhar (1997). Their curvature factor is site-specific and varies with leaf area index, fraction of diffuse irradiance and leaf-nitrogen content. However, the effect in the C budget is low and generally lower than 5% (e.g. Meister *et al.*, 1987). In our study, the good agreement obtained between simulated and measured ecosystem  $GPP$  suggests that the departure from the optimal profiles of leaf properties may have led to limited simulation errors.

#### The 'big-leaf' approach for the surface conductance

Use of combination equation to simulate canopy evaporation is based on the hypothesis that leaf properties can be quantitatively scaled up to the canopy. As a result, with respect to energy and water flux, the canopy can be treated as a 'big-leaf'. Inversion of the Penman–Monteith equations resulted in a drought-induced decline of canopy conductance, which varied between 0.75 and 0.1  $\text{cm s}^{-1}$ . However,  $g_{\text{cwmax}}$  values reached in the absence of water stress, i.e. when  $RWC$  was close to 1 and  $\Psi_p$  was close to zero, were largely higher than 1  $\text{cm s}^{-1}$ . Owing to the selection method we used, these data have not been retained in our analysis. But, this value is largely lower than the maximum canopy conductance measured in late fall by Valentini *et al.* (1991) over a Mediterranean macchia dominated by *Q. ilex* (2.8  $\text{cm s}^{-1}$ ). It disagrees with those proposed in the reviews of Kelliher *et al.* (1995) and of Schulze *et al.* (1994) for the superclasses temperate deciduous forest (2.07  $\text{cm s}^{-1}$ ) and sclerophyllous shrubland (2.2  $\text{cm s}^{-1}$ ). It is closer to the value of 1.4  $\text{cm s}^{-1}$  corresponding to the superclass temperate evergreen broadleaf forest. By comparison, the likelihood value for the maximum stomatal conductance,  $g_{\text{swmax}}$ , observed over the light-saturated phase of the day, which was reached in the absence of any drought stress in *Q. ilex*, was 0.65  $\text{cm s}^{-1}$ . Rhizopoulou & Mitrakos (1990) recorded 0.7  $\text{cm s}^{-1}$ , whereas Sala & Tenhunen (1994) found a value of 0.65  $\text{cm s}^{-1}$  in agreement with the review of Acherar & Rambal (1992).

Canopy conductance computed in the way described above was low. This finding has been extensively observed in boreal coniferous forests (Moore *et al.*, 2000) and seemed to hold in some Mediterranean-type

ecosystems (Reichstein *et al.*, 2002). The computed values are approximately two times lower than those reported in the literature. This discrepancy needs some explanation: the big-leaf approach in which  $g_{\text{cw}}$  may be derived from  $g_{\text{sw}}$  by the equation  $g_{\text{cw}} = g_{\text{sw}} LAI$  seems to hold for a large range of leaf area index. Granier *et al.* (2000) intensively tested this hypothesis on needleleaf evergreen and broadleaf deciduous canopies with  $LAI$  reaching 6. The big-leaf approach failed in a dense *Q. ilex* canopy. Teixeira Filho *et al.* (1998) observed that the model yields very good results if total  $LAI$  is replaced by the sun-exposed fraction. Part of the discrepancy is due to the fact that at high water availability, the response curve of  $g_{\text{swmax}}$  to  $\Psi_p$  is rather vertical. Gúñas *et al.* (2002) wrote 'the *Quercus (ilex)* in their study) and *Pistacia* species achieved 50% stomatal closure before showing a reduction in predawn relative water content of the leaves'. The last point deals with the time-course of  $g_{\text{swmax}}$  with leaf aging. The default value that we proposed was obtained on young mature leaves. The evergreen canopy we worked with is composed of both cohorts, one composed with new mature leaves or current growth leaves and the second cohort composed of 1-year-old leaves with a lower stomatal conductance. Damesin (1996) reported a one-third decline with maximal values of 0.6  $\text{cm s}^{-1}$  for current year leaves, whereas she observed 0.4  $\text{cm s}^{-1}$  for 1-year leaves.

The large amplitude of  $RWC$  and  $\Psi_p$  that we observed made it possible to analyze the mechanism by which conductance is regulated over the entire range of functioning in *Q. ilex*. Some of the  $\Psi_p$  values are even higher than the limit proposed for Mediterranean evergreen oaks by Rambal & Debussche (1995). Both  $g_{\text{cwmax}}$  and ecosystem  $GPP_{\text{day}}$  decline with  $RWC$ . The threshold where the decline is faster occurred at ca. 0.65. Zero values were obtained at  $RWC = 0.41$  for  $g_{\text{cwmax}}$  and at 0.45 for  $GPP_{\text{day}}$ . These values are in agreement with Arneth *et al.* (1998b), who found in a dry *P. radiata* plantation that  $g_{\text{cwmax}}$  zeroed at 0.35 with a threshold at 0.6–0.65 and that  $F_c$  seemed affected at higher  $RWC$  values. If we fix the zero value at 0.4, we obtain results close to those of Granier *et al.* (2000). They proposed a generic model with a threshold of 0.4 for the  $REW$ , a threshold independent of species and soil type.

During the onset of drought, a decrease in maximum conductance was recorded, which was closely related to the predawn water potential and fitted to an inverse function. Leaf-level relations of the same type were first obtained by Pereira *et al.* (1987) on *Eucalyptus globulus*, and further by Acherar & Rambal (1992) on four Mediterranean oaks including *Q. ilex* and by Damesin *et al.* (1998) for *Q. ilex* and *Q. pubescens*. This decrease in maximum conductance was also observed *in situ* for

*Q. ilex* by Sala & Tenhunen (1994) in two contrasting ecological situations: ridge and valley locations, and further pooled in one data set. However, these latter authors found that it could be described by a unique linear relation.  $\Psi_p$  has been successfully used in predicting leaf stomatal closure in mixed canopy dominated by *Q. ilex* (Teixeira Filho *et al.*, 1998) and in Farquhar-type leaf photosynthesis models (Infante *et al.*, 1999; Sala, 1999) for the same species growing in water-limited environments.

Our last point deals with the ability of *Q. ilex* to maintain a high conductance at low  $\Psi_p$ . We observed  $g_{cwmax}$  of  $0.1 \text{ cm s}^{-1}$  at  $\Psi_p$  near  $-5 \text{ MPa}$ . This is true for the tree species under study, and also true for other evergreen oak trees or shrubs such as *Q. coccifera* and *Q. suber* around the Mediterranean Sea and *Q. dumosa* in California (Tenhunen *et al.*, 1987; Hasting *et al.*, 1989). This is also true in Mediterranean deciduous oak trees: *Q. pubescens* (Damesin & Rambal, 1995), *Q. douglasii* (Xu & Baldocchi, 2003). This functional trait facilitates maintenance of a positive carbon balance even under very dry conditions.

## Conclusion

Our results demonstrate the importance of soil water deficits on canopy water and carbon exchanges on ecosystems that experience seasonal drought such as Mediterranean-type ecosystems. The approach that we used enabled us to take into account the functional relationships controlling ecosystem fluxes. As stated by Jarvis (1995), such an approach is not mechanistic because it does not link environmental factors with stomatal functioning at the biochemical level. Nevertheless, its empirical character makes it useful for the interpretation of field observations at the leaf level and prediction of both conductance and gross assimilation at the canopy level. On the whole, and in spite of the simplifying assumptions used in the representation of the canopy: big-leaf, clumping, the equations we identified are useful for predicting interactions between Mediterranean *Q. ilex* woodland and the environment and for interpreting water and carbon exchange measurements.

In conclusion, here we advocate the use of methods in which scale-down and scale-up approaches are cyclically applied and strategically designed to address practical problems (Rambal *et al.*, 1992). Many works refer to the standard practices normally used in resolving problems of changes of scale (Elheringer & Field 1992). Bottom-up and top-down approaches tend to be opposed or even exclude one another. Paraphrasing (Root & Schneider 1995), we suggest to further use 'scale-down embedded in scale-up' approaches.

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