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

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4. Parameterisation and application of a two-source evapotranspiration model in a Scots pine stand under Mediterranean mountain conditions

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Despite all the computations
You could just dance to a rock ‘n’ roll station
And it was alright.

Rock & Roll, The Velvet Underground

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Abstract
Forest evapotranspiration has been the object of diverse modelling approaches in hydrology and ecophysiology, using representations of canopy structure and surface control of evaporation of varied complexity. In this paper we used a two-source evapotranspiration model to predict canopy transpiration ($E_c$) and soil evaporation ($E_s$) in a Scots pine under Mediterranean mountain conditions. Canopy stomatal conductance ($G_c$), obtained from stand scale sap flow, was modelled using a semiempirical Jarvis-type model, whereas soil resistance to evaporation was expressed as a function of superficial soil moisture. The evapotranspiration model was first used with a calibration of the $G_c$ model on sap flow data obtained during the year 2004 using quantile regression techniques (boundary-line parameterisation). Validation using two more datasets (2003 and 2005) showed how the model tended to overpredict $E_c$ under ample soil moisture conditions. Model performance with respect to daily values of $E_c$ for the years 2003 and 2004 was within the usual range for this kind of models, but validation against data from the year 2005 showed a poor agreement with observations. Maximum modelled $E_c$ rates were 0.7 mm day$^{-1}$ with the ratio $E_s/E_c$ being typically under 0.3 during the growing season. A Generalized Likelihood Uncertainty Estimation (GLUE) calibration was carried out using 2003 and 2004 data. The best parameter set in the GLUE analysis showed better overall performance than the boundary-line parametrisation. Parameters representing reference stomatal aperture and sensitivity to vapour pressure deficit ($D$) were the most relevant, whereas those controlling the response to soil moisture deficit (SMD$_{0-30}$) only appeared sensitive when calibration against 2003 data was done. Combining calibration results from 2003 and 2004 showed how predictive uncertainty was reduced and the value of some parameters was constrained. Nevertheless, despite the exhaustive exploration of the parameter space in the GLUE analysis, the model continued to yield a poor performance for the year 2005, suggesting that the Jarvis algorithm cannot adequately simulate long-term $E_c$ under the studied conditions.

Resum
L’evapotranspiració dels boscos ha estat objecte de diverses aproximacions en la modelització hidrològica i ecofisiològica, utilitzant representacions de l’estructura de la capçada i del control de l’evaporació de complexitat variable. En aquest article s’utilitza un model d’evapotranspiració de dues capes pel tal de predir la transpiració de la capçada ($E_c$) i del sòl ($E_s$) en una pinada de pi roig en condicions de muntanya Mediterrània. La condutància estomatòtica de la capçada ($G_c$), obtinguda a partir de les mesures de flux de saba a escala de cobert, fou simulada utilitzant un model semi-empèric de tipus Jarvis, mentre que la resistència del sòl a la evaporació s’expressà en funció de la humitat superficial d’aquest. El model d’evapotranspiració s’utilitzà en primer lloc calibrant el model de $G_c$ amb les dades de flux de saba obtingudes durant l’any 2004 realitzant una parametrisació per envolvents (boundary-line parametrisation) emprant tècniques de regressió de quantils. La validació amb els dos altres jocs de dades (2003 i 2005) mostrà que el model tendia a sobreestimar $E_c$ en un ample rang de condicions d’humitat del sòl. Els resultats del model pel que fa als valors diaris de $E_c$ per als anys 2003 i 2004 estaven dins d’un rang acceptable per aquests tipus de models, però la validació amb les dades de l’any 2005 mostrà poca concordança amb les observacions. Les taxes màximes d’$E_c$ foren de 0.7 mm dia$^{-1}$ amb una raó $E_s/E_c$ normalment per sota de 0.3 durant el període de creixement. Una calibració de tipus GLUE (Generalized Likelihood Uncertainty Estimation) s’utilitzà per calibrar el model utilitzant les dades del 2003 i del 2004. El millor conjunt de paràmètres obtingut en l’anàlisi GLUE presentà millor resultats que la parametrisació per envolvents. Els paràmètres representant l’obertura estomatòtica i la sensibilitat al déficit de pressió de vapor ($D$) foren els més rellevants, mentre que els que controlen la resposta al déficit hidric del sòl (SMD$_{0-30}$) només resultaren sensibles quan es calibrà amb el joc de dades del 2003. La combinació dels resultats de les calibracions de 2003 i 2004 mostrà una reducció de la incertesa en la prediccio i una restricció del rang d’alguns paràmeters. Tot i l’exhaustiva exploració de l’espai de paràmètres en l’anàlisi
Use of a two-source evapotranspiration model in a Scots pine stand

GLUE, el model continuà simulant amb poca exactitud l’any 2005, suggerint que l’algoritme de Jarvis no és capaç de simular correctament la $E_c$ a llarg termini en les condiciones estudiades.

Introduction

Forest evapotranspiration constitutes an important fraction of total water loss from land surfaces into the atmosphere and therefore, adequate models of this process are needed for accurate predictions of water balance in forested watersheds. These models incorporate the active role of vegetation in regulating water vapour fluxes into the atmosphere, establishing a close link between disciplines such as hydrology, micrometeorology and ecophysiology.

Models of forest evapotranspiration usually combine some form of the Penman-Monteith equation (Monteith 1965) with a representation of the surface and aerodynamic controls in a resistance network (Huntingford et al. 1995; Raupach and Finnigan 1988). These models basically differ in the degree of detail in the physical representations of the canopy (the complexity of the resistance network) and the description of physiological regulation of transpiration by forest canopies.

When canopies are uniform and closed, spatially aggregated models (‘big-leaf’) often yields satisfactory results (Bernhofer et al. 1996). At the other end, multi-layer schemes offer more realistic descriptions of canopy structure of heterogeneous surfaces (Raupach and Finnigan 1988), but these approaches are computationally and data-intensive and become less appropriate as spatial scale increases (McNaughton and Jarvis 1991). A compromise between multi-layer and ‘big-leaf’ approaches are multiple-source interactive models, which allow the consideration of two (Shuttleworth and Wallace 1985) or more surfaces (Brenner and Incoll 1997) with different properties and distinct values of vapour pressure deficit. Furthermore, they include the interaction between overstory and understory fluxes and its consequences on within-canopy microclimate (Daamen and McNaughton 2000).

Whereas soil surface resistance depends mainly on soil physical properties and surface soil moisture (Wallace 1995) and is frequently modelled using simple relationships with topsoil water content (Camillo and Gurney 1986), complex empirical and semiempirical representations of plant surface resistance, are widely used within these model structures. Plant surface resistance is mainly determined by stomatal aperture, which can be modelled based solely on water relations (Jarvis 1976), or coupling transpiration and photosynthesis (Leuning 1995). Coupled models are preferred when the purpose is to model water vapour and CO$_2$ exchange between the canopy and the atmosphere (Hanson 2004). The Jarvis algorithm, although purely empirical has been shown to
represent adequately the underlying physiological processes of stomatal regulation in hydrological applications (Mackay et al. 2003a).

Canopy transpiration and soil evaporation measurements are commonly used to parameterise plant (Granier et al. 1996) and soil resistances (Domingo et al. 1999). Parameter optimisation of Jarvis-type models involves separate boundary-line analysis of canopy stomatal conductance \( G_s \) against the individual meteorological variables (Chambers et al. 1985). However, it has long been recognised that for soil-vegetation-atmosphere transfer models (Franks et al. 1997), and in general for environmental models (Beven and Freer 2001) many parameter sets will yield acceptable simulations. The Generalized Likelihood Uncertainty Estimation (GLUE) procedure was developed to deal with this equifinality problem (Beven and Binley 1992). This methodology is also useful to investigate the sensitivity of the parameters within the model, the associated predictive uncertainty, and the effect of incorporating new data into the calibration procedure (Beven and Freer 2001).

In this study, carried out in a Scots pine (Pinus sylvestris L.) forest under Mediterranean mountain conditions, we used soil evaporation and sap flow measurements to parameterise the corresponding soil and plant surface resistances to evaporation in a two-layer interactive model scheme (Shuttleworth and Wallace 1985). The main aims of the study were (a) to parameterise soil and plant surface resistance in a two-layer interactive model (Shuttleworth and Wallace 1985) applied to a Mediterranean Scots pine stand, (b) to investigate the performance of the model under varying meteorological and soil moisture conditions, using independent sap flow datasets for validation, (c) to examine parameter sensitivity and predictive uncertainty using the GLUE procedure and (d) to compare the widely-used boundary-line calibration of Jarvis-type \( G_s \) models with the results from the GLUE calibration.

**Table 1.** List of relevant symbols in the model with their respective units.

<table>
<thead>
<tr>
<th>Description</th>
<th>Symbol</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy structure and aerodynamics</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy height</td>
<td>( h )</td>
<td>m</td>
</tr>
<tr>
<td>Leaf Area Index</td>
<td>LAI</td>
<td>m² m⁻²</td>
</tr>
<tr>
<td>Plant Area Index</td>
<td>PAI</td>
<td>m² m⁻²</td>
</tr>
<tr>
<td>Roughness length</td>
<td>( z_0 )</td>
<td>m</td>
</tr>
<tr>
<td>Radiation transfer and soil heat flux</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Above-canopy net radiation</td>
<td>( R_n )</td>
<td>W m⁻²</td>
</tr>
<tr>
<td>Canopy net radiation</td>
<td>( R_{nc} )</td>
<td>W m⁻²</td>
</tr>
<tr>
<td>Below-canopy net radiation</td>
<td>( R_{nc} )</td>
<td>W m⁻²</td>
</tr>
<tr>
<td>Parameter describing leaf angle distribution</td>
<td>( x )</td>
<td>adimensional</td>
</tr>
<tr>
<td>Extinction coefficient for ( R_n )</td>
<td>( \kappa )</td>
<td>adimensional</td>
</tr>
<tr>
<td>Sun zenith angle</td>
<td>( \theta_s )</td>
<td>rad</td>
</tr>
<tr>
<td>Other meteorological variables</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vapour pressure deficit at reference height</td>
<td>( D_r )</td>
<td>kPa</td>
</tr>
<tr>
<td>Vapour pressure at reference height</td>
<td>( e_r )</td>
<td>kPa</td>
</tr>
</tbody>
</table>
Table 1 (continued).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temperature at reference height</td>
<td>$T_a$</td>
<td>°C</td>
</tr>
<tr>
<td>Wind speed at reference height</td>
<td>$u$</td>
<td>m s$^{-1}$</td>
</tr>
</tbody>
</table>

**Resistance network**
- Plant surface resistance                     | $r_s$  | s m$^{-1}$    |
- Soil surface resistance                       | $r_s'$ | s m$^{-1}$    |
- Plant aerodynamic resistance                  | $r_a$  | s m$^{-1}$    |
- Soil aerodynamic resistance                   | $r_a'$ | s m$^{-1}$    |
- Resistance between reference height and effective source/sink height | $r_a''$ | s m$^{-1}$    |

**Parameters of the G, model**
- Canopy stomatal conductance                   | $G_s$  | mm s$^{-1}$   |
- Reference conductance at 1 kPa                | $G_{ref}$ | mm s$^{-1}$   |
- Absolute sensitivity of $G_s$ to $\ln D$      | $m$    | mm s$^{-1}$ ln kPa$^{-1}$ |
- $R_s$ at half-saturation of $G_s$             | $R_{0.5}$ | W m$^{-2}$    |
- Threshold of $G_s$ reduction with SMD$_{0.30}$ | $s$    |               |
- Fraction of $G_s$ when SMD$_{0.30}=1$         | $f_s$  |               |
- Time optimum for $G_s$                        | $t_{opt}$ | hours         |
- Minimum time for $G_s$                        | $t_{min}$ | hours         |
- Maximum time for $G_s$                        | $t_{max}$ | hours         |
- Optimum air temperature for $G_s$             | $T_{opt}$ | °C            |
- Minimum air temperature for $G_s$             | $T_{min}$ | °C            |
- Maximum air temperature for $G_s$             | $T_{max}$ | °C            |

**Soil parameters**
- Soil moisture (0-30 cm)                       | $\theta_{0.30}$ | cm$^3$ cm$^{-3}$ |
- Soil moisture deficit (0-30 cm)               | SMD$_{0.30}$ | adimensional |
- Soil moisture deficit (30-60 cm)              | SMD$_{30-60}$ | adimensional |
- Soil moisture 0-15 cm                         | $\theta_{0.15}$ | cm$^3$ cm$^{-3}$ |
- Soil moisture (0-15 cm) at field capacity     | $\theta_{0.15, FC}$ | cm$^3$ cm$^{-3}$ |
- Parameter of soil surface resistance equation | $b_1$   | s m$^{-1}$    |
- Parameter of soil surface resistance equation | $b_2$   | adimensional  |
- Saturated vapour pressure at soil temperature | $e_{Ys}$ | kPa           |

**Other**
- Canopy transpiration                          | $E_c$  | mm s$^{-1}$, mm day$^{-1}$ |
- Soil evaporation                               | $E_i$  | mm s$^{-1}$, mm day$^{-1}$ |
- Model efficiency                               | $E_i$  | adimensional    |

**Material and methods**

**Site and Stand characteristics**

The experimental plot is part of the Vallcebre research area (42° 12’ N, 1° 49’ E), located in the Eastern Pyrenees (NE Spain). Climate is sub-Mediterranean, with an average air temperature of 7.3 °C (measured at 1440 m.a.s.l.) and 924 mm of annual rainfall (Gallart et al. 2002). The present landscape is mainly a mosaic of mesophilous grassland of the *Aphyllantion* type and patches of Scots pine, which colonised old agricultural terraces after their abandonment (Poyatos et al. 2003).
The studied 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). Biometric characteristics of the stand are summarized in Chapter 1.

**Meteorological, soil moisture and sap flow measurements**

Above-canopy meteorology, soil moisture and sap flow by the heat dissipation method (Granier 1985) were measured continuously between June 2003 and August 2005. For details of meteorological, soil moisture and sap flow instrumentation see Chapter 1. Additional measurements of soil moisture between 30 and 60 cm depth were taken on a weekly basis, at two locations in the plot, using the TDR technique. Upscaling of sap flow measurements in individual trees was done according to the measured radial patterns in each particular tree (see Chapters 2 and 3 for details).

Below-canopy net radiation \( (R_{ns}) \) and soil heat flux \( (G) \) were also measured during July and August of year 2005 to parametrize the radiative transfer within the canopy. We obtained the estimates of \( R_{ns} \) by averaging the measurements from three net radiometers (Q7, REBS, Seattle, WA, USA) randomly placed above the forest soil. Four soil heat flux plates (HFT-3, REBS, Seattle, WA, USA) were also installed to measure soil heat flux at a depth of 0.08 m, and above each plate, a set of soil thermocouples (TCAV, Campbell Scientific) inserted at 0.02 and 0.06 m depth, measured the average temperature of the soil layer above the plates. Consecutive differences in soil temperature, together with soil moisture estimates for the topsoil (see next section) and bulk density of the soil, were used to calculate the energy stored above the heat flux plates (Massman 1992), which was added to the flux measured by the plates to obtain total soil heat flux. A general description of the meteorology during the period of study can be found in chapter 5.

**Soil evaporation measurements**

Soil evaporation measurements were carried out following the recommendations by Daamen et al. (1993). Six PVC cylinders of 11.8 cm in diameter and 15 cm depth were randomly installed in the forest soil (lysimeter cases). For each measurement date, a set of 4-6 soil cores were extracted by hammering a PVC tube (diameter 10.8 cm, 15 cm long) into the soil in a nearby location. These lysimeters were sealed with a PVC cap and then inserted into the lysimeter cases, covering the top of the lysimeter with a plastic mesh to
avoid measurement errors due to litterfall. The lysimeters were weighed in the morning between 7:00-8:00 solar time, and then in the evening (18:00-19:00 solar time). Soil evaporation rate was then calculated from the difference in weight divided by the time between measurements.

**Model parameterisation**

We refer to the appendix for the basics of the Shuttleworth and Wallace (1985) evapotranspiration model, but in this section we will detail the modifications in the radiative transfer and resistance parameterisation that will be included in this particular application, and the different datasets used for model calibration.

A micrometeorological dataset obtained during July 2005 was used to parameterise radiative transfer within the canopy. Stand-scale sap flow, meteorological and soil moisture data measured during the year 2004 (Table 2) were used to parameterise canopy surface resistance ($r_s$) and soil evaporation measurements, as described above, were used to parameterise soil surface resistance ($r_s$).

**Table 2.** Characteristics of the datasets used in the calibration and validation stages. One-year periods are shown for better comparison of meteorological conditions across years.

<table>
<thead>
<tr>
<th>Year</th>
<th>Period (days)</th>
<th>Average $D_r$ (kPa)</th>
<th>Rainfall (mm)</th>
<th>$\theta_{0.30}$ (cm$^3$cm$^{-2}$)</th>
<th>Calibration procedures</th>
</tr>
</thead>
<tbody>
<tr>
<td>2003</td>
<td>205-365</td>
<td>0.68</td>
<td>433</td>
<td>0.24</td>
<td>Validation</td>
</tr>
<tr>
<td>2004</td>
<td>1-362</td>
<td>0.56</td>
<td>644</td>
<td>0.23</td>
<td>Calibration*</td>
</tr>
<tr>
<td>2005</td>
<td>1-212</td>
<td>0.77</td>
<td>312</td>
<td>0.19</td>
<td>Validation</td>
</tr>
</tbody>
</table>

* Equal-length periods

- 2003- July 2003
- 2004- June 2004
- 2004- July 2003
- 2005- June 2004

* The model has been validated separately for each year and therefore calibration data has also been used for validation.

\* Dataset used to update likelihoods obtained when the model was constrained with 2004 data.

**Parameterisation of radiation transfer and soil heat flux**

Above-canopy net radiation ($R_n$) was partitioned between canopy ($R_{n,c}$) and soil ($R_{n,s}$) according to:

$$R_n^c = R_n - R_n^s$$

and the penetration of net radiation through the canopy was modelled according to Lambert-Beer’s law

$$R_n^c = R_n \exp(-\kappa f(\Theta_s, x) \cdot PAI)$$
Where the function \( f \) accounted for the variation of the extinction coefficient with sun zenith angle (\( \Theta_s \)) and leaf angle distribution (\( \kappa \)), \( \kappa \) is the extinction coefficient for net radiation and PAI is plant area index. We assumed an elliptical leaf angle distribution,

\[
f(\Theta_s,\kappa) = \frac{\left(1 + \tan^2 \Theta_s\right)^{0.5}}{x + 1.774(x+1.182)^{-0.733}}
\]

with the value \( x=3.33 \) obtained from previous measurements in nearby stands (Llorens and Gallart 2000) and a maximum plant area index of 2.8, which was obtained by adding to LAI a fixed amount corresponding to branch fraction (Llorens and Gallart 2000). The value of \( \kappa \) was obtained using measured \( R_{ns} \) and \( R_n \) and inverting the model described above for a period with clear skies (days 215-218, August 2005).

A preliminary analysis of the correlation between measured soil heat flux (\( G \)) and radiation reaching the soil showed that \( G \) was better correlated with \( R_{ns} \) at \( t-4 \), that is, soil heat flux lagged one hour behind radiative input at the forest soil. Therefore, we used this 1h-lagged \( R_{ns} \) soil water content in the first 15 cm \( (\theta_{b-15}) \) and air temperature as independent variables to predict soil heat flux using a multiple regression model fitted to measured data (days 214-221, August 2005).

**Parameterisation of soil surface resistance**

We calculated the soil surface resistance to evaporation \( r_s \) as:

\[
r_s = \frac{0.622p / P}{E_s} (e_{s1} - e_r) - r_d
\]

Where \( p \) is air density (kg m\(^{-3}\)), \( P \) is atmospheric pressure in kPa, \( e_{s1} \) is saturated vapour pressure in soil pore space, \( e_r \) is vapour pressure at the reference height, \( E_s \) is soil evaporation (kg m\(^{-2}\) s\(^{-1}\)) and \( r_d \) is aerodynamic resistance (s m\(^{-1}\)). We used soil evaporation measured with microlysimeters to calculate \( r_s \) and then relate its value to the soil moisture conditions of the plot.

Overall, we obtained fifteen estimates of \( r_s \) in four measurement dates along the year 2005 (19 and 20th of May, 4th of August and 24th August). Soil surface resistance estimated for each lysimeter and measuring date was related to volumetric soil moisture of the lysimeter \( (\theta_{b-15}) \) fitting a power relationship,

\[
r_s = b_1 \left( \frac{\theta_{b-15}}{\theta_{b-15, FC}} \right)^{b_2}
\]

Where \( \theta_{b-15, FC} \) is the corresponding value of soil moisture at field capacity \( (\theta_{b-15, FC} = 0.35 \text{ cm}^3 \text{ cm}^{-3}, \text{C.Rubio, personal communication}) \).
A linear relationship between the average soil moisture of the plot in the upper 30 cm ($\theta_{0-30}$) and soil moisture in the lysimeters was fitted in order to directly relate the value of soil surface resistance to the average soil moisture measured continuously.

Parameterisation of canopy resistance

Canopy surface resistance ($r_c$) is defined in the model as

$$r_c = \frac{1}{G_c\text{LAI}}$$

(6)

Where $G_c$ is canopy stomatal conductance and LAI is stand leaf area index (see Chapter 2 for details on LAI estimation). Leaf area index seasonal variation was assessed from observations of the onset of leaf elongation in late spring and leaf senescence in autumn, and assuming that a fixed fraction of maximum LAI remains throughout late autumn, winter and early spring (Beadle et al. 1982).

Canopy stomatal conductance was first calculated from stand-scaled sap flow measurements and meteorological data, using the inversion of the Penman-Monteith equation for well coupled canopies (Whitehead and Jarvis 1981) and assuming no capacitance effects. Then, $G_c$ was parameterised using data with $D_3$>0.6 kPa to minimise the measurements errors in $G_c$ (Ewers and Oren 2000), as a function of the main meteorological variables (Jarvis 1976):

$$G_c = G_{c,\text{max}}(D) f_1(R_n) f_2(T) f_3(SMD_{0-30}) f_4(t)$$

(7)

Maximum conductance $G_{c,\text{max}}$ was constrained by a series of functions which depend on single environmental variables: $R_n$, air temperature ($T$), soil moisture deficit ($SMD_{0-30}$) and time of day ($t$). Soil moisture deficit in the upper 30 cm ($SMD_{0-30}$) was calculated using $\theta_{0-30}$ as described in Granier and Loustau (1994) (see also Chapter 2).

Parameterisation of individual constraint functions of a given variable in $G_c$ multiplicative models is usually carried out by selecting different subsets of data where the rest of the variables present in the model are considered non-limiting for $G_c$. However we used a sequential calibration procedure using boundary-line analysis (Granier et al. 2000; Lagergren and Lindroth 2002). We began parametrising the response of $G_c$ to $D$ by means of a boundary-line analysis, using the quantile regression of the 99th quantile for that purpose (procedure rq, R Statistical Software v. 2.0.1; see Chapters 1 and 5 for more detailed descriptions of the procedure). The model suggested by Oren et al. (1999) was adopted:

$$G_{c,\text{max}} = G_{c,\text{ref}} - m \ln D$$

(8)
We selected the intercept and slope of the 99th quantile fit as representative of the relationship between \( G \) and \( \ln D \) at optimal conditions, and therefore of the coefficients \( G_{s,\text{ret}} \) and \( m \), respectively. After estimating \( G_{s,\text{max}} \) we looked for a relationship between the ratio of the measured conductance and \( G_{s,\text{max}} \) and \( R_n \). If this ratio was greater than 2, the value was omitted from the analysis. Nonlinear quantile regression (procedure nlrq in the quantreg package, R Statistical Software v.2.0.1) was used in this case to find the fit for the 99th quantile of the equation

\[
f_1(R_n) = \frac{R_n}{R_{n,0.5} + R_n}
\]

(9)

Where the parameter \( R_{n,0.5} \) represents the value of \( R_n \) at which \( f(R_n) \) is 0.5.

Based on the prior information on the reduction of conductance with soil moisture in \( P.\text{sylvestris} \) (Irvine et al. 1998; Lagergren and Lindroth 2002) we established a soil moisture function with two parameters: \( s \), defining the threshold beyond which soil water supply limits transpiration and \( f_0 \) meaning the fraction of transpiration that is still sustained when \( \text{SMD}_{0-30} = 0 \):

\[
\text{SMD}_{0-30} < s \Rightarrow f_2(\text{SMD}_{0-30}) = 1
\]

\[
s < \text{SMD}_{0-30} < 1 \Rightarrow f_2(\text{SMD}_{0-30}) = \left( \frac{f_0 - 1}{1 - s} \right) \text{SMD}_{0-30} + \left( \frac{1 - sf_0}{1 - s} \right)
\]

(10)

The resulting relationship equals 1 when \( \text{SMD}_{0-30} < s \), reduces to \( f_0 \) when \( \text{SMD}_{0-30} = 0 \) and shows a linear decrease when \( s < \text{SMD}_{0-30} < f_0 \). We chose the value of the parameters \((s=0.6, f_0=0.4)\) according to previous studies in the same plot (Poyatos et al. 2005).

The constraint function for temperature was found in an analogous way to \( f(R_n) \) (i.e. relating the ratio \( G/(G_{s,\text{max}}(D) \cdot f_i(R_n) \cdot f_i(\text{SMD}_{0-30})) \) to air temperature, using a quadratic function with \( T_{\text{min}}, T_{\text{max}} \) and \( T_{\text{opt}} \) being minimum, maximum and optimum temperatures, respectively

\[
f_3(T) = \frac{(T - T_{\text{min}})}{(T_{\text{opt}} - T_{\text{min}})} \cdot \frac{(T_{\text{max}} - T)}{(T_{\text{max}} - T_{\text{opt}})}
\]

(11)

Finally as an additional dependence of \( G \), with time of day was observed in previous analysis, a quadratic function equivalent to that of temperature was included to correct for this effect, where a time optimum \( t_{\text{opt}} \) was also found using nonlinear quantile regression:

\[
f_4(t) = \frac{(t - t_{\text{min}})}{(t_{\text{opt}} - t_{\text{min}})} \cdot \frac{(t_{\text{max}} - t)}{(t_{\text{max}} - t_{\text{opt}})}
\]

(12)
Parameterisation of aerodynamic resistances

Three aerodynamic resistances are involved in the model, \( r_a \) and \( r_{so} \), canopy and soil aerodynamic resistances, respectively and the resistance between reference height and the effective source/sink height, \( r_{so} \). All of them were calculated assuming a logarithmic wind profile, K-theory for eddy and characteristic leaf dimensions and canopy structure for Scots pine (Shuttleworth and Gurney 1990). A more detailed description of the resistance network of this model can be found in Iritz et al.(1999).

Parameter conditioning using Generalised Likelihood Uncertainty Estimation (GLUE)

We carried out an alternative calibration using the GLUE methodology, which do not consider the existence of a global optimum parameter set, due to the uncertainties present both in models and experimental data, and the inherent complexity of high dimensional parameter spaces (Beven and Binley 1992). Instead, GLUE analysis retains, from a large sample of parameter sets, the models which are considered to be acceptable simulators of our system (or ‘behavioural’).

Thirty thousand Monte Carlo simulations were performed using parameters randomly sampled from uniform distributions with ranges established according to previous experience and preliminary Monte Carlo runs. All the parameters in the G, submodel and canopy roughness length \( (z_0) \), which affects aerodynamic resistance, were included in the GLUE analysis (Table 3). In addition to the initial calibration data (2004), the GLUE procedure was also carried out using data from another period in 2003 (Table 2). Each simulation was performed using the available meteorological data and the resulting simulated \( E_c \) was compared to experimentally measured \( E_c \) from sap flow. We computed model efficiency \( (E_i) \) (Nash and Sutcliffe 1970) for each run and used it as a likelihood measure:

\[
L(\theta_j | Y) = 1 - \frac{\sum_{j=1}^{N} (O_i - P_i)^2}{\sum_{j=1}^{N} (O_i - \overline{O})^2}
\]

\( L(\theta_j | Y) \) is the likelihood measure for the \( j \)th parameter set \( (\theta_j) \) conditioned on the observations \( Y \). The right hand-side of the equation equals model efficiency, which equals 1 for a perfect fit, with \( O_i \) and \( P_i \) being observed and predicted values of \( E_c \) at the \( i \)th time step and \( \overline{O} \) the mean of observed values. Model efficiency, whose maximum value equals 1 for a perfect fit, was calculated both at the 15-min step and also on a daily basis. Models
with $E_t < 0$ were rejected for further analysis, as negative efficiencies are no better than a mean of the data (Nash and Sutcliffe 1970).

**Table 3.** Range of parameters and the distribution from which they were sampled in the GLUE analysis

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Distribution</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$G_{\text{wref}}$</td>
<td>Uniform</td>
<td>2.0</td>
<td>10.0</td>
<td>mm s$^{-1}$</td>
</tr>
<tr>
<td>$m$</td>
<td>Uniform</td>
<td>1.0</td>
<td>10.0</td>
<td>mm s$^{-1}$ kPa$^{-1}$</td>
</tr>
<tr>
<td>$R_{0.05}$</td>
<td>Uniform</td>
<td>0</td>
<td>500</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$s$</td>
<td>Uniform</td>
<td>0.2</td>
<td>1</td>
<td>Adimensional</td>
</tr>
<tr>
<td>$f_0$</td>
<td>Uniform</td>
<td>0</td>
<td>1</td>
<td>Adimensional</td>
</tr>
<tr>
<td>$t_{\text{opt}}$</td>
<td>Uniform</td>
<td>4</td>
<td>20</td>
<td>hour (decimal)</td>
</tr>
<tr>
<td>$T_{\text{opt}}$</td>
<td>Uniform</td>
<td>5</td>
<td>35</td>
<td>°C</td>
</tr>
<tr>
<td>$z_0$</td>
<td>Uniform</td>
<td>1.0</td>
<td>6.0</td>
<td>m</td>
</tr>
</tbody>
</table>

Scatter plots displaying $E_t$ against each parameter’s value were examined to infer the characteristics of the parameter space with regard to model performance. Two different efficiency thresholds for behavioural models were considered for the instantaneous and daily cases (0.5 and 0.75 respectively). Then, cumulative likelihood distributions of the parameters for behavioural and non-behavioural models were compared to assess the sensitivity of each parameter. If uniform distributions were obtained (straight lines), the parameter was considered to be insensitive to the likelihood measure chosen.

Predictive uncertainty bounds were estimated at each time step by ranking the outputs from behavioural models according to their likelihood weights, and deriving a cumulative distribution (Franks and Beven 1997). Likelihood weights had been previously obtained by rescaling the efficiencies of the behavioural models in order that their sum was 1. We chose the 5% and 95% quantiles of the resulting distribution to represent predictive uncertainty related to model calibration with 2004 and 2003 data.

The GLUE methodology allows the combination of likelihoods when more data becomes available. In this study, the initial parameter conditioning on 2004 data was updated with the results from the GLUE analysis for 2003, making use of the Bayes theorem to combine both likelihoods:

$$L(\Theta_j | Y) = L(Y | \Theta_j) L_0(\Theta_j)/C (14)$$

Where $L_0(\Theta_i)$ is a prior likelihood measure for the parameter set $\Theta_i$, $L(Y | \Theta_j)$ is the likelihood measure obtained when conditioning on the new data set, $L(\Theta_j | Y)$ is the posterior likelihood after updating, and $C$ is a scaling constant. This principle was also applied when carrying out the individual GLUE analysis, but as uniform distributions for parameters were assumed, $L_0(\Theta_i)$ would have been constant and equation 14 would have yielded the same posterior as equation 13. In this way, if a parameter set performed badly in one of the calibration periods (i.e. it was non-behavioural), the combined likelihood yielded a value of zero.
Results

Radiative transfer

The value of the extinction coefficient $\kappa$ obtained from the inversion of the radiation transfer submodel was ca. 0.9, yielding an acceptable simulation of the overall diurnal course of net radiation within the forest. However, this approach could not reproduce the radiation peaks in the observations, which approached 250 W m$^{-2}$ in some occasions (Fig.1). These differences had little impact on aggregated fluxes at the daily level. Soil heat flux was modelled according to the obtained multiple regression fit ($G=0.19 R_{	ext{ns}}(t-4)+2.61 T+188.5101; R^2=0.58; N=480$). Again, the peaky dynamics of $G$ could not be simulated, but the overall daily dynamics, which ranged between -40 and 60 W m$^{-2}$ was appropriately represented (Fig.1).

Optimisation of soil and canopy resistances
Figure 2. Results of the canopy stomatal conductance parameterisation by boundary-line analysis, showing the resulting functions (thick lines) and the data points used to fit them. The best parameter sets obtained in the GLUE parameter conditioning on 2004 data (dashed lines) and 2003 data (thin lines) are also shown.

Soil evaporation measurements used for parametrising soil surface resistance were always below 0.15 mm day⁻¹. The value of $r_s$ was related to soil moisture at the top 15 cm, relative to water content at field capacity, using a potential function (Eq. 5) with coefficients $b_1=8.74$ and $b_2=-2.55$ ($R^2=0.43, N=14, P=0.011$).
With respect to canopy stomatal conductance, the boundary line analysis results showed that $G_s$ decreased strongly with $D_r$ increased very rapidly for low values of radiation and achieved its temperature and time optimums halfway between the considered minimum and maximum temperatures and time of day, respectively (Fig. 2). All the constraint functions in the Jarvis model showed maximum values close to unity.

Validation of the optimised model

The relationship between measured and observed values of instantaneous $E_c$ varied across years (Fig. 3), with slopes significantly different from unity in all cases and positive intercepts (Table 5). Model performance was specially poor for the year 2005, both at the 15-min and daily time-scales.
We examined diurnal simulations under different evaporative demand and soil moisture conditions (Figs 4). The model overestimated $E_c$ when SMD$_{0-30}$ was low and $D_r$ was below 2 kPa during a period in the summer of 2004 (Fig. 4b). Under conditions of high $D_r$ and SMD$_{0-30}$, model overestimation was less marked, although when high $D_r$'s were reached (up to 4 kPa), the predicted values of $E_c$ declined rapidly and did not track the diurnal course of the observations (Fig. 4a). For a period with varying soil moisture and evaporative demand conditions during the year 2005, simulations and observed data were in close agreement only when SMD$_{0-30}$ was high and considerable overestimation was found again when SMD$_{0-30}$ was low (Fig. 4c). Model residuals decreased with $D_r$ and $T$ at low to intermediate values of these variables, but then increased at higher $D_r$ and $T$ (data not shown). We did not find any relationship between model residuals and SMD including deeper soil layers (0-60 cm) obtained from weekly TDR measurements (data not shown).
Aggregated daily $E_c$ was generally overestimated by the model, especially during the year 2005 (Figs. 5,6), with $E_r$ showing a negative value (Table 5). Maximum soil evaporation rates were estimated at less than 0.7 mm day$^{-1}$, although values between 0.1 and 0.5 mm day$^{-1}$ were the most frequent (Fig. 6). On a daily basis, the ratio between modelled $E_s$ and measured $E_c$ was below 0.3 for almost 80% of the days during the growing season (days 140-300), but this changed for non-growing season days, with only a 40% of the days with $E_s/E_c$ fractions below 0.3.
**Figure 3.** Observed and modelled $E_c$, with (a) the parameterisation obtained from the boundary line analysis and (b) the best parameter set obtained in the GLUE analysis with 2004 data. Fitting results in table 4.
Figure 4. Observed and modelled Ec rates during three periods with varying soil moisture deficit and vapour pressure deficit conditions.
Figure 5. Observed and modelled values of daily canopy transpiration ($E_c$) for each year during the measuring period, obtained with the boundary-line parameterisation (a) or the best parameter set in the GLUE analysis with data from the year 2004. Fitting results in table 4.

**GLUE analysis: parameter space**

For the year 2004, 15% of the simulations (more than 4500 parameter sets) had positive efficiencies when calculated at the 15-min level, but this number doubled (more than 10000 models) when daily efficiencies were considered. Maximum model efficiencies were greater when calculations of model performance were done at the daily time scale than for the instantaneous values (ca. 0.65 and 0.86, respectively). However, plots of parameter values against $E_t$ calculated at the daily level showed very similar patterns to plots with $E_t$ calculated at the 15-min level. Given this similarity between results at the 15-min and daily time scales, further analysis and discussion will be based on daily likelihoods.

The boundary-line parameterisation of the $G_t$ model yielded worse results in terms of model efficiency than the best parameter set obtained in the GLUE calibration with data from the year 2004 (Table 5). Using this parameter set, simulated values did not overestimate $E_c$ so much as the model with the boundary-line parameterisation (Fig. 4, 5). However, the resulting functions from the best parameter sets for the two conditioning periods (2004 and 2003) did not represent the envelope relationships of $G_t$ against the individual variables in the $G_t$ model (Fig. 1).
Table 4. Parameter values for the optimised model using the boundary-line technique and results for the best parameters sets from GLUE analysis for 2003 and 2004 data.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>2003</th>
<th>2004</th>
<th>2005</th>
</tr>
</thead>
<tbody>
<tr>
<td>$G_{x, ref}$</td>
<td>5.96</td>
<td>4.56</td>
<td>3.23</td>
</tr>
<tr>
<td>$m$</td>
<td>4.11</td>
<td>2.84</td>
<td>1.25</td>
</tr>
<tr>
<td>$R_{n, 0.5}$</td>
<td>30.00</td>
<td>239.39</td>
<td>398.36</td>
</tr>
<tr>
<td>$s$</td>
<td>0.60</td>
<td>0.21</td>
<td>0.73</td>
</tr>
<tr>
<td>$f_0$</td>
<td>0.4</td>
<td>0.575</td>
<td>0.40</td>
</tr>
<tr>
<td>$t_{opt}$</td>
<td>10.52</td>
<td>13.03</td>
<td>14.58</td>
</tr>
<tr>
<td>$T_{opt}$</td>
<td>17.0</td>
<td>7.98</td>
<td>17.93</td>
</tr>
<tr>
<td>$z_0$</td>
<td>3.60</td>
<td>3.19</td>
<td>3.34</td>
</tr>
</tbody>
</table>

Figure 6. Time series of modelled and observed canopy transpiration ($E_c$) and modelled soil evaporation ($E_s$) during the whole study period. Modelled results for with the boundary-layer (BL) parametrisation and the best parameter set obtained in the GLUE calibration are shown.
Figure 7. Parameter conditioning of the evapotranspiration model with sap flow data from year 2004 after 30,000 Monte Carlo realisations. (a) Plot of daily efficiency against parameter values included in the GLUE analysis (Table 2). Only simulations with $E_r > 0$ are shown. (b) Cumulative likelihood distribution of the parameters, for behavioural ($E_r > 0.75$) and non-behavioural models ($E_r < 0.75$).

The range of the parameters $G_{s,ref}$ and $m$ were noticeably constrained by the 2004 calibration data (Fig. 7a), as efficiency peaked at values of $G_{s,ref}$ about 4.5 mm s$^{-1}$ and values of $m$ of about 3.0 mm s$^{-1}$ ln kPa$^{-1}$. The derived value of relative sensitivity of $G_s$ to ln
D \( (m/G_{s,ref}) \) was likewise constrained at values lower than unity. For the rest of parameters, behavioural models were found across the whole sampled range (Fig. 7a). Differences in the cumulative distributions between behavioural (525 parameter sets in total) and non-behavioural models were clear for \( G_{s,ref} \) and \( m \), and also evident for \( T_{opt} \) and \( f_0 \) (Fig. 7b). Values of \( T_{opt} \) in the central part of the sampled range (15-25 °C) were less probable than values at the extremes, and for \( f_0 \) values were mostly between 0.3 and 0.9. Remarkably, the parameters controlling the response to radiation and the threshold for reduction due to soil moisture deficits (\( R_{ir,0.5} \) and \( s \)) showed identical, almost uniform distributions for behavioural and non-behavioural sets (Fig. 7b).

Substantial differences were found when the model was constrained against 2003 data (Fig. 8), beginning with the number of behavioural models (160 parameter sets), which was much lower than in the previous GLUE exercise for the year 2004. The scatter plots showed that positive model efficiencies were less frequent at large values of \( G_{s,ref} \) and \( m \) (\( G_{s,ref} > 6.0 \) and \( m > 5.0 \)) (Fig. 8a). Contrarily to what occurred when conditioning on 2004 data, parameter sets with high \( E_t \) were found with \( T_{opt} \) values around the middle of the chosen parameter range. This was reflected in the narrower interquartile range for \( T_{opt} \) when the model was conditioned on 2003 data (Fig. 9).

The two parameters defining the response of \( G_t \) to soil moisture deficit were more sensitive when calibrating against 2003 data. Only the ranges of \( G_{s,ref} \), \( m \), and to a lesser extent, \( f_0 \) changed appreciably with the data period used for conditioning (Fig. 9). The interquartilic ranges of the parameters in the models retained after updating the 2004 calibration with 2003 data, showed how \( m/G_{s,ref} \) was constrained around 0.6, and \( s \) and \( f_0 \) were centered around 0.6 and 0.45, respectively (Fig. 9).

We examined the interactions between pairs of parameters in the behavioural sets obtained with 2003 and 2004 data (Fig. 10). For 2004, it can be seen that at a given value of \( m/G_{s,ref} \), between 0.6-0.8, higher \( E_t \) concentrated in a wide range of \( s \) and \( f_0 \). As we have shown earlier, higher efficiencies lie in the extreme values of \( T_{opt} \). If behavioural models conditioned on 2003 data are considered, the regions with the best model performance could be clearly delimited.
Figure 8. Parameter conditioning of the evapotranspiration model with sap flow data from year 2003 after 30,000 Monte Carlo realisations. (a) Plot of daily efficiency against parameter values included in the GLUE analysis (Table 3). Only simulations with $E_t > 0$ are shown. (b) Cumulative likelihood distribution of the parameters, for behavioural ($E_t > 0.75$) and non-behavioural models ($E_t < 0.75$).
GLUE analysis: predictive uncertainty

The uncertainty bounds calculated solely on the basis of behavioural models for the 2004 calibration period, encompassed much of the data during 2003 and 2004, although the width of the bounds was very large for the 2003 dry summer (Fig. 1a). When validating against data from the year 2005 (validation), most of the observations fell out of the 5% and 95% uncertainty envelope or were close to the inferior 5% limit (Fig. 11a). This envelope was narrower when calculated with likelihoods conditioned on 2003 data, but then observations during the 2004 period lied closer to the superior limit instead of being centered around the uncertainty limits (Fig. 11b).

**Figure.** 9. Average value (dots) and interquartilic range (bars) of selected parameters for behavioural models when the model was constrained with 2004 data, 2003 data and the obtained likelihoods from both GLUE analysis were combined (C) as described in the text.

When the initial parameter conditioning on 2004 data was used as prior information and likelihoods were updated according to new likelihoods resulting from conditioning on the 2003 period, only 44 parameter sets were retained. Uncertainty bounds calculated on the basis of these parameter sets (Fig. 11c), were very similar to the ones obtained only from behavioural models of the 2003 period. We also represented an example of the uncertainty envelopes for 15-min data based on daily likelihood values for the initial calibration period (2004) (Fig. 12a) and the resulting updated likelihood weights (Fig. 12b), showing the narrower uncertainty envelopes with updated likelihoods. Therefore, although updating likelihoods with more calibration data has been shown to reduce predictive uncertainty in $E_c$ estimates, there continues to be a poor performance of the model during 2005 (Figs. 10, 11) even when information from two distinct periods are incorporated in the calibration procedure.
Table 5. Performance of the model in terms of $E_c$ calibrated using the boundary-line technique or using the best parameter set from the GLUE analysis. Number of observations ($N$), slope, intercept and coefficient of determination ($R^2$) of the linear regression between observed and simulated values for different periods at the instantaneous and daily time scales.

<table>
<thead>
<tr>
<th></th>
<th>Boundary-line parameterised</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th>Best parameter set GLUE 2004</th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$N$</td>
<td>$R^2$</td>
<td>Slope</td>
<td>Intercept</td>
<td>$E_r$</td>
<td>$R^2$</td>
<td>Slope</td>
<td>Intercept</td>
</tr>
<tr>
<td>15-min</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>2003</td>
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<td>4.80E-06</td>
<td>0.23</td>
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<td>2004</td>
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<td>0.67</td>
<td>1.05</td>
<td>1.20E-06</td>
<td>0.42</td>
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<td>2005</td>
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<td>0.49</td>
<td>1.08</td>
<td>1.70E-05</td>
<td>-1.35</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>2003</td>
<td>151</td>
<td>0.85</td>
<td>0.98</td>
<td>0.250</td>
<td>0.38</td>
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<tr>
<td>2004</td>
<td>323</td>
<td>0.85</td>
<td>0.72</td>
<td>0.140</td>
<td>0.64</td>
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</tr>
<tr>
<td>2005</td>
<td>160</td>
<td>0.75</td>
<td>0.96</td>
<td>0.500</td>
<td>-1.23</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

4. Discussion

Forest floor micrometeorology and soil evaporation

Our simple representation of radiative transfer and soil heat flux did not allow for a precise simulation of understorey fluxes. However, the use of the Lambert-Beer law did not preclude the obtention of appropriate descriptions of diurnal dynamics of net radiation at the forest floor (Fig. 1). The observed $k$ for net radiation was larger than the values reported elsewhere for other canopy types (Kustas and Norman 1999). The multiple regression approach employed to derive $G$ reproduced correctly the influence of soil moisture and the lag between radiative input and soil heat flux (Kustas and Norman 1999), but the fine resolution simulation of $G$ requires more precise estimations of $R_{ns}$. 
Figure. 10. Values of model efficiency of behavioural models conditioned on 2004 data (left column) and 2003 data (right column) related to the values of pairs of parameters in the $G_m$ model.

Measured soil evaporation during 2005 was very low as a result of the low soil moisture content in the topsoil layers. However, the obtained function of soil surface resistance, similar in overall shape to other formulations found in the literature (Domingo et al. 1999; Wallace 1995), resulted in typical maximum values of $E_s$ when the soil was wet, close to those found by Wilson et al. (2000). Similarly, soil evaporation rates in a Douglas-fir stand also increased from 0.2 to 0.4 mm day$^{-1}$ when soil moisture conditions changed from dry to wet (Schaap and Bouten 1997).
Figure 11. Uncertainty bounds (5% and 95%) of daily transpiration \( (E_c) \) (shaded area) in relation with observed \( E_c \) (black line). (a) For behavioural models when conditioned on 2004 data, (b) for behavioural models when conditioned on 2003 data and (c) for sets retained after updating 2004 likelihoods with 2003 data.
Boundary-line parametrisation of canopy stomatal conductance and model performance

We succeeded in calibrating a Jarvis-type $G_t$ model using a sequential parameterisation procedure based on boundary-line relationships (Granier et al. 2000; Lagergren and Lindroth 2002). The general shape of the functions was in accordance with previous findings on these species (Stewart 1988), with the addition of a function introducing variation due to time of day. This dependence on time has been reported in other studies (Huntingford and Cox 1997; Uddling et al. 2005), and been attributed to circadian rhythms (Mencuccini et al. 2000) or responses to leaf water potential (Dolman and Burg 1988).

Although overall good fits were obtained with the boundary-line parameterisation for daily $E_c$ during 2003 and 2004 (calibration dataset), the model did not simulate adequately 2005 data. Despite acceptable model performance for daily data in 2003 and 2004, the diurnal courses of modelled $E_c$ significantly departed from the observations under certain environmental conditions. The model considerably overestimated $E_c$ when soil moisture deficit was not limiting and extremely high $D_i$'s also caused the model to reduce $G_t$ excessively, leading to underestimation of $E_c$. One could argue that the soil moisture deficit function was arbitrarily assigned based on previous knowledge, and only checked visually against data. Several tests of alternative functions for $f(D)$ and $f(SMD_{0-30})$ were carried out, but results did not significantly improve overall model performance.

Apart from the issue of finding the appropriate constraint functions, other unaccounted factors might be limiting model performance under the wide range of environmental conditions included in this study. Severe physiological changes must have taken place in the year 2005 to explain the poor performance of the model during this period. This will be further discussed in the next sections. Furthermore, multiplicative models bear additional problems concerning interactions and compensation among parameters (Fig. 9), due the inevitable correlation among some of the input variables (mainly $T$, $R_v$ and $D$). Given the complexity of the issues exposed (parameter search, assessment of model structure and parameter interactions), we used the GLUE methodology to explore them further.
Figure 12. Uncertainty bounds (5% and 95%) for instantaneous $E_c$ rates based on behavioural simulations using daily likelihoods for the three periods in Fig. 4. (a) Bounds based on behavioural simulations for the model conditioned on 2004 data and (b) posterior likelihoods after updating with 2003 data (see text for details). Observations are also shown.

Parameter space in the $G_i$ model

Before discussing the issues regarding model behaviour, we will first acknowledge that Monte Carlo sampling of the parameter space yielded parameter sets with better overall efficiencies than the boundary-line analysis calibration (Table 5), despite not representing
the envelope functions as proposed in the original model formulation (Jarvis 1976). For the case of radiation, for example, the respective function in the model does not reach a maximum value of 1. Although leaf level stomatal conductance saturates at a certain value of irradiance (Ng and Jarvis 1980), when dealing with entire trees and canopies, higher irradiance means that more leaves open their stomata, contributing to increase $G_i$ (Martin et al. 1997). The high correlation between $D$ and $T$ can also lead to mutual compensation between $G_{i,max}(D)$ and $f_3(T)$ (Ogink-Hendriks 1995). Mutual compensation between functions or the absence of other relevant factors in the $G_i$ model may be responsible for these relationships not being truly envelopes.

Parameter conditioning on 2004 and 2003 data revealed that some information was missing on the behaviour of the system in the 2004 data set. When using these data for calibration, parameters controlling the soil moisture response of $G_i$ appeared insensitive. Moreover, the $T_{opt}$ parameter was constrained on values in the extreme of the temperature range, in clear disagreement with usual reports of this temperature optimum for *P. sylvestris* (Beadle et al. 1985; Stewart 1988). When the model was calibrated with 2003 data, however, both parameters in $f_3(SMD_{30})$ became sensitive, specially $f_0$ and $T_{opt}$ lied preferentially between 15 and 20 °C.

The reason why the model was sensitive to soil moisture parameters only when calibrated against 2003 data, can be explained because although a wide range of $SMD_{30}$ conditions existed in 2004 (Chapter 4), the summer drought of 2003 was longer and more intense. This fact suggests that a lengthy dry period is necessary to detect $G_i$ sensitivity to soil moisture parameters. It may also point at the need for including the influence of the whole soil profile on physiological regulation of $G_i$, not only the upper 30 cm, although some studies show that tree response to drought is closely related to moisture availability in the first centimeters of the soil, where fine root density is highest (Warren et al. 2005). The use of internally stored water in sapwood tissues to meet evaporative demand could also allow for $G_i$ to remain open, decoupling stomatal dynamics from the increase in soil moisture deficits (Meinzer 2002).

Even though model residuals were not related to $SMD_{30-60}$ the $f_0$ parameter, representing the fraction of $G_i$ remaining after $SMD_{30}=1$ showed a lower range when the model was conditioned on 2003 data (Table 5). A lower $f_0$ means a stronger reduction of $G_i$, when there is no water availability in the upper soil, which might be linked to more depleted water reserves in deeper soil layers during 2003 (Rubio, unpublished data).

The average value of $G_{i,ref}$ for the behavioural models was 12% lower when the model was conditioned on 2003 data, while the reduction in $m$ was higher (35%). This resulted in a decline in $m/G_{i,ref}$, and therefore, during the dry period, trees did not show an enhanced sensitivity of $G_i$ to $D$ (see Chapter 5). There is a noticeable similarity between the obtained
Use of a two-source evapotranspiration model in a Scots pine stand

The ratio m/G_{\text{ref}} and the theoretical slope between G_{\text{ref}} and G_{\text{ref}} (dG_{\text{d}}/d\ln D = 0.6) predicted by a hydraulic model assuming stomatal control of water potential to avoid cavitation and corroborated against an extensive survey of leaf and canopy-level observations (Oren et al. 1999). Recent studies have shown the consistency of Jarvis-type model of G_{\text{c}} with hydraulic theory (Mackay et al. 2003a), although they still recognise the influence of parameter compensation (Mackay et al. 2003b).

**Limitations of Jarvis-type stomatal conductance models**

Jarvis-type G_{\text{c}} models are attractive because of their simplicity and the relatively good results in predicting transpiration fluxes from forest canopies. For this reason, they have been widely incorporated into terrestrial biosphere models (Mackay et al. 2003a) and land-surface exchange schemes (Bartlett et al. 2003). Nevertheless, in very few occasions have this kind of models been tested again data comprising more than one growing season (but see Lagergren and Lindroth (2002)) and including such variable conditions as shown in this study. Model performance at the daily scale was relatively good during the years 2004 (calibration period) and 2003, but failed to simulate adequately E_{\text{c}} for the year 2005. In addition, the simulation of diurnal courses of E_{\text{c}} was not satisfactory under certain environmental conditions.

Using the GLUE methodology we explored the predictive uncertainty of the evapotranspiration model, and concluded that, even when we included additional data from a dry period to calibrate the model, it continued to overestimate E_{\text{c}} during 2005. Therefore, the current model structure could not account for the physiological processes regulating year-round E_{\text{c}} in the studied stand.

Stomatal conductance has been shown to be tightly linked to hydraulic conductance of the soil-to-leaf pathway (Irvine et al. 1998; Meinzer and Grantz 1990) which in turn can be reduced by drought-induced (Tyree and Sperry 1988) or freeze-thaw embolisms (Sperry and Sullivan 1992). Both situations must have surely arisen during the study period, which included an acute summer drought (summer 2003), and an extense dry period between autumn 2004 and spring 2005, which included some days of extremely low temperatures (see Chapter 5). This drought during a period when soil moisture is usually recovered from summer water deficits, is extremely unusual and might have been responsible for the mortality of Scots pine individuals in locations close to the study area, but at lower elevations, at the end of the spring 2005 (personal observation). In addition, the no consideration of capacitances in the trunk, may have precluded the correct simulation of diurnal courses of E_{\text{c}} when water stored in sapwood is being used to meet evaporative demand (Phillips et al. 1997). Recent comparisons among different G_{\text{c}} modelling schemes,
showed that coupled models and more physically-based approaches with less calibration effort may produce better results than the Jarvis multiplicative model (Falge 2005; Misson et al. 2004).

*Why a two-layer model?*

Two-source evapotranspiration models based on the principles by Shuttleworth and Wallace (1985), applied to forest ecosystems, usually show superior performance than single-layer models, especially under wetter conditions when the contribution from the soil is highest (Fisher et al. 2005). This model encloses in a simple formulation, a physically sound description of within canopy processes, allowing interaction between fluxes from different surfaces and making the model very versatile to apply in forest with different densities, cover fractions and LAI (Daamen and McNaughton 2000). However, we only validated the model against the canopy component of evapotranspiration and we could not test the validity of the model to simulate whole forest evapotranspiration. With whole surface vapour exchange (eddy covariance methods) or continuous $E_t$ measurements (automatic lysimeters, within-canopy eddy covariance) the model could be further assessed, using the framework of the GLUE methodology. This method would permit a more robust model evaluation against multiple model outputs, as previously done for similar multi-source models predicting water and CO$_2$ fluxes (Mo and Beven 2004).

Finally, an important shortcoming of our particular formulation of the physiological regulation of plant transpiration is its dependence on soil moisture as an input variable. This fact limits model applicability in hydrology, as this variable is unavailable from standard meteorological stations, and the model would be greatly improved by the inclusion of a soil water balance subroutine. More realistic descriptions of plant and soil resistances and how they vary with evaporative demand and water supply (for example Williams et al. 2001), may also be included in these two-source evapotranspiration models to generalize their applicability across different stands and varying conditions.

**Conclusions**

We have shown how plant and soil controls on evaporation can be modelled within a two-source modelling framework using sap flow an soil evaporation measurements. The use of one-year sap flow data to calibrate the $G_s$ submodel with quantile regression techniques yielded good fits at the daily level. However, this parameterisation technique was not superior to a stochastic Monte Carlo sampling of the parameter space.
Examination of diurnal courses also showed consistent $E_c$ overestimations when soil moisture deficit was low. Modelled soil evaporation represented a small fraction of total evaporation during the growing season. The GLUE methodology showed that the parameters controlling reference stomatal aperture and sensitivity to $D$ were the most relevant. Additional calibration with data including a long dry period was needed to detect substantial sensitivity of soil moisture parameters. This fact supports the view that Jarvis-type $G_t$ models require extensive datasets to be tuned. Regardless of the calibration procedure, the model could not predict $E_c$ adequately during the year 2005, pointing at the inadequacy of multiplicative $G_t$ models to simulate physiological regulation of transpiration under the conditions of evaporative demand and soil moisture characteristic of Mediterranean mountain areas.

**Appendix. Model structure**

The energy budget for the whole surface under consideration can be expressed as

$$A = \lambda E + H = R_a - G$$  \hspace{1cm} (A1)

Where $A$ is available energy at the surface and $H$ is sensible heat flux. In this formulation physical and biochemical energy storage components have been omitted. Similarly, the specific energy balance at the forest soil is given by

$$A_s = \lambda E_s + H_s = R_a - G$$  \hspace{1cm} (A2)

According to the resistance network, vapour pressure deficit at the canopy source height $D_0$ is calculated as (Shuttleworth and Wallace, 1985)

$$D_0 = D + \{\Delta A - (\Delta + \gamma)\lambda E \}_{r_a}^\prime / \rho c_p$$  \hspace{1cm} (A3)

Where $\Delta$ is the slope of saturation vapour pressure curve against temperature, $\gamma$ is the psychrometric constant, and $\lambda$ is latent heat of vaporisation of water.

Then, evapotranspiration from the two sources can be expressed as a function of this $D_0$

$$\lambda E_c = (\Delta A_c + \rho c_p D_0 / r_a^\prime \{\Delta + \gamma (1 + r_s^\prime / r_a^\prime \})^{-1}$$ \hspace{1cm} (A4)

$$\lambda E_s = \{\Delta (A - A_s) + \rho c_p D_0 / r_a^\prime \{\Delta + \gamma (1 + r_s^\prime / r_a^\prime \})^{-1}$$ \hspace{1cm} (A5)

Considering that

$$\lambda E = \lambda E_c + \lambda E_s$$ \hspace{1cm} (A6)

And after some algebra manipulation (Shuttleworth and Wallace, 1985) we get

$$\lambda E = C_c PM_c + C_s PM_s$$ \hspace{1cm} (A7)

Where $PM$ terms are pseudo Penman Monteith combination equations:
\[ PM_{c} = \frac{\Delta A_{c} + (\rho c_{p} D_{r} - \Delta r_{c}^{e} A_{r})/(r_{c}^{a} / r_{c}^{c})}{\Delta + \gamma[1 + r_{c}^{e} / (r_{c}^{a} + r_{c}^{c})]} \] (A8)

\[ PM_{s} = \frac{\Delta A + [\rho c_{p} D_{r} - \Delta r_{s}^{e} (A - A_{r})]/(r_{s}^{a} / r_{s}^{c})}{\Delta + \gamma[1 + r_{s}^{e} / (r_{s}^{a} + r_{s}^{c})]} \] (A9)

And coefficients \( C_{c} \) and \( C_{s} \) result from the combination of resistances and thermodynamic parameters \( \Delta \) and \( \gamma \):

\[ C_{c} = [1 + R_{c} R_{a} / R_{c}(R_{c} + R_{a})]^{-1} \] (A10)

\[ C_{s} = [1 + R_{s} R_{a} / R_{s}(R_{s} + R_{a})]^{-1} \] (A11)

Where

\[ R_{a} = (\Delta + \gamma)r_{a}^{a} \] (A12)

\[ R_{c} = (\Delta + \gamma)r_{c}^{c} + \gamma r_{c}^{e} \] (A13)

\[ R_{s} = (\Delta + \gamma)r_{s}^{s} + \gamma r_{s}^{e} \] (A14)

Equation A7 allows the calculation of A3, and in turn, the contribution of each source to total evapotranspiration is obtained with equations A4 and A5. The calculations begin using \( D_{0} \) instead of \( D_{0} \) then \( D_{0} \) is calculated using equation A3. An iterative process begins until the difference between consecutive \( D_{0} \) values is less than 0.005 kPa.

**References**


