RATP: a model for simulating the spatial distribution of radiation absorption, transpiration and photosynthesis within canopies: application to an isolated tree crown

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ABSTRACT
The model RATP (radiation absorption, transpiration and photosynthesis) is presented. The model was designed to simulate the spatial distribution of radiation and leaf-gas exchanges within vegetation canopies as a function of canopy structure, canopy microclimate within the canopy and physical and physiological leaf properties. The model uses a three-dimensional (3D) representation of the canopy (i.e. an array of 3D cells, each characterized by a leaf area density). Radiation transfer is computed by a turbid medium analogy, transpiration by the leaf energy budget approach, and photosynthesis by the Farquhar model, each applied for sunlit and shaded leaves at the individual 3D cell-scale. The model typically operates at a 20–30 min time step. The RATP model was applied to an isolated, 20-year-old walnut tree grown in the field. The spatial distribution of wind speed, stomatal response to environmental variables, and light acclimation of leaf photosynthetic properties were taken into account. Model outputs were compared with data acquired in the field. The model was shown to simulate satisfactorily the intracrown distribution of radiation regime, transpiration and photosynthetic rates, at shoot or branch scales.

Key-words: Juglans regia L.; 3D architecture; ecophysiology; intracanopy scale; model description; walnut tree.

INTRODUCTION
Models of carbon and water exchanges between the vegetation and the atmosphere can be used for applications ranging from assessment of carbon sequestration, net primary production and water use at the landscape scale to resource capture and use at plant or organ scale. Although every application involves the same processes, the assumptions used in the models may have different implications according to the scale of investigation. In the case of forests, orchards or agricultural crops, modelling carbon and water fluxes at the canopy scale has been successful in the investigation of production potentials and the effect of environmental factors on yield (e.g. Monteith 1977; Varlet-Grancher et al. 1982; Jarvis & Leverenz 1983). However, variability in canopy attributes, i.e. between plants or between organs, may largely contribute the value of plant production. For example, there is the case of fruit distribution in horticultural crops and knot distribution in timber trees. On the one hand, fruit quality depends on local assimilate supply, water status and fruit temperature (Génard & Huguet 1996), i.e. a number of local properties related to microclimate in the fruit zone (Tustin, Hirst & Warrington 1988). On the other hand, knot distribution results from axillary shoot development, the morphology of which depends on local carbon supply (Sprugel, Hinckley & Schaap 1991; Takenaka 1994; Kellomäki & Strandman 1995). In both cases, spatial variations in fruit and wood properties are likely to be related to local exchanges between the vegetation and the atmosphere.

Several three-dimensional (3D) models simulating carbon and/or water exchanges between plants and the atmosphere at the intracanopy scale have been proposed in the literature. In these models, canopy structure was abstracted as an array of 3D cells (also called voxels) (Myneni 1991; Chen et al. 1994; Desmarez et al. 2000) or geometrical shapes accounting for individual plants (e.g. Thorpe et al. 1978; Wang & Jarvis 1990). These models were aimed at scaling up from the leaf to the canopy, i.e. simulating carbon and/or water exchanges at the canopy scale as the result of the 3D canopy structure and leaf properties. To our knowledge, such models have not been tested and used at the intraplant scale. In this article, we propose a 3D model combining radiation transfer, energy balance and photosynthesis, for simulating carbon sources and water losses at the intracanopy scale. The model does not include soil water balance and uptake of water by roots. The model was tested against light, transpiration and photosynthesis measurements at the shoot or branch scale within the crown of an isolated walnut tree.

MATERIALS AND METHODS
Model description
The model RATP (radiation absorption, transpiration, photosynthesis) is aimed at simulating the spatial distribution

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of radiation, transpiration and photosynthesis in vegetation canopies including one or several plant components. Inputs for the model are canopy geometry, micrometeorological driving variables and properties of plant components. Canopy geometry is described as an array of 3D cells, the size of which is user-defined according to x, y and z-axes (Fig. 1).

Each cell may be empty or contain area of one or several canopy components. The latter can be defined in a very flexible way: organ classes (e.g. leaves, woody parts and fruit), leaf classes (e.g. according to age), plants or vegetation species making a mono- or multiple-species canopy. In practice, canopy components are generally leaves. Each occupied cell is characterized by the area density (m² m⁻³) of every canopy component in the cell. The grid of cells also discretizes the soil surface into a set of zones which exchange radiation with the vegetation (Fig. 1).

Driving variables include incident radiation above the canopy and air characteristics within the canopy. Incident radiation includes the sun direction, and solar radiation split into photosynthetically active radiation (PAR; 400–700 nm) and near infrared radiation (NIR; above 700 nm), and each into direct and diffuse components, and atmospheric radiation. Air characteristics are temperature, water vapour and CO₂ partial pressure and wind speed. They can be entered as uniform, vertical profiles or at the 3D cell scale.

Properties of the plant components include physical properties (i.e. orientation angles characterized by inclination distribution, scattering coefficient in PAR and NIR wavebands, and the relationship between wind speed and leaf boundary layer conductance) and physiological properties (i.e. stomatal and photosynthesis responses to environmental conditions in case of leaves).

Model outputs are the radiation balance, organ temperature, carbon gain and water loss of the shaded and sunlit area of each foliage component at the 3D cell scale.

The principal assumptions used in the model are the turbid medium analogy for radiation computations, and the use of empirical relationships for the plant responses: leaf boundary layer conductance as a function of wind speed, stomatal conductance as a function of environmental variables, intracanopy distribution of leaf nitrogen, leaf photosynthetic capacity as a function of nitrogen.

### Interception of solar radiation

The model RATP has been developed from Sinoquet & Bonhomme’s (1992) radiative transfer model, where the canopy is treated as a turbid medium. Incident radiation is abstracted as a set of directional sources accounting for direct and diffuse radiation, i.e. one source of direction Ωsun and a set of sources regularly spaced in the sky vault, respectively. Light interception in each direction Ω is inferred from a sample of beams regularly spaced above the canopy, i.e. the array of 3D cells. The distance between two consecutive beams along x and y-axes is user-defined and usually chosen so that 25 beams enter the top side of each 3D cell. The fate of a beam of direction Ω in the vegetation canopy is computed: (i) by identifying the sequence of 3D cells visited by the beam; (ii) by deriving the beam path length within the visited cells; and (iii) by applying Beer’s law to calculate beam extinction within any visited cell. Steps (i) and (ii) are performed from geometrical computations (e.g. see Kimes & Kirchner 1982). After crossing the kth visited cell, the non-intercepted fraction Pjk of beam energy is

\[ P_{jk} = \exp \left[ - \sum_{k'=1}^{k} \sum_{j'=1}^{j} G_{jk'}(\Omega) a_{jk'} \delta_{k'} \right]. \]  

where \( k' = 1, \ldots, k \) is the sequence of visited cells from the top of the canopy. The coefficient \( G_{jk}(\Omega) \) is the projection of unit leaf area of component \( j \) in cell \( k \), onto a plane perpendicular to beam direction \( \Omega \) (G-function, Ross 1981). \( G_{jk}(\Omega) \) depends on direction \( \Omega \) and the angle distribution of component \( j \) in cell \( k \). The term \( a_{jk} \) is area density (m² m⁻³) of component \( j \) in cell \( k \). Distance \( \delta_k \) is the length of beam path in cell \( k \).

Within cell \( k \), intercepted radiation is partitioned between the \( J(k) \) vegetation components, assuming that phytoelements are uniformly, randomly and independently distributed within the cell. The fraction of beam energy \( P_{jk} \) intercepted by component \( j \) in cell \( k \) may thus be written (Sinoquet & Bonhomme 1991)

\[ P_{jk} = \exp \left[ - \sum_{k'=1}^{k} \sum_{j'=1}^{j} G_{jk'}(\Omega) a_{jk'} \delta_{k'} \right] \times \left( 1 - \exp \left[ - \sum_{j'=1}^{j} G_{jk'}(\Omega) a_{jk'} \delta_{k'} \right] \right) \times \frac{G_{jk} a_{jk}}{\sum_{j'=1}^{j} G_{jk'} a_{jk'}}. \]  

In Eqn 2, the three terms of the right member, respectively, account for: (i) the fraction of non-intercepted beam energy before entering cell \( k \); (ii) the fraction of energy
intercepted by all vegetation components in cell \( k \); and (iii) the fraction of energy intercepted by component \( j \) in cell \( k \).

Computation of beam interception is used to derive radiation exchange coefficients \( C_{S\rightarrow R} \) between sources \( S \) and receptors \( R \). Radiation sources are the sky (i.e. direct and diffuse fraction of incident radiation), as well as foliage components and the soil surface since they scatter a fraction of intercepted radiation. Receptors are vegetation and the soil surface since they intercept radiation, and the sky for reflected radiation. Exchange coefficients \( C_{S\rightarrow R} \) are progressively built by adding the contribution of beams coming from source \( S \) when they encounter receptor \( R \).

Direct radiation is characterized by the sun direction \( \Omega_{\text{sun}} \). The exchange coefficient between the sun (i.e. for direct radiation) and foliage of component \( j \) in cell \( k \) can be written

\[
C_{b0\rightarrow jk} = \sum_{\text{beams}} P_{jk}(\Omega_{\text{sun}})S_{\text{beam}},
\]

where \( b0 \) refers to the sun beam, and the sum concerns the beams crossing cell \( k \). \( S_{\text{beam}} \) is the horizontal section of beams, which depends on beam spacing. \( C_{b0\rightarrow jk} \) must be computed when the sun direction \( \Omega_{\text{sun}} \) changes. The directional distribution of diffuse incident radiation is computed after a standard overcast sky (SOC, Moon & Spencer 1942). The exchange coefficient between the sky (i.e. for sky diffuse radiation) and foliage of component \( j \) in cell \( k \) can be written

\[
C_{d0\rightarrow jk} = \sum_{\Omega} \left[ I_{d0}(\Omega) \sum_{\text{beams}} P_{jk}(\Omega)S_{\text{beam}} \right] + \sum_{\Omega} I_{d0}(\Omega),
\]

where \( d0 \) refers to the incident diffuse radiation. The first sum refers to the sky discretization in a set of directionally radiation fluxes \( I_{d0}(\Omega) \). Thus \( C_{d0\rightarrow jk} \) includes radiation distribution for sky diffuse radiation. Similar considerations allow one to derive exchange coefficients for scattered radiation. Scattering by phytoelements and the soil surface is assumed isotropic (see Sinoquet & Bonhomme 1992). Note that the exchange coefficients for scattered radiation do not include leaf reflectance and transmittance, so that they can be used for any waveband with the isotropic scattering assumption.

Exchange coefficients are used to compute radiation fluxes intercepted in the 3D cells, i.e. including both the interception of incident radiation and multiple scattering. The flux \( I_{jk} \) intercepted by each component \( j \) in each cell \( k \) is written using a formalism close to the radiosity method (Ozisik 1981)

\[
I_{jk} = I_{b0}C_{b0\rightarrow jk} + I_{d0}C_{d0\rightarrow jk} + \sum_{k' = 1}^{K} \sum_{j' = 1}^{J} I_{jk'} \rho_{jk'}C_{jk'\rightarrow jk} + \sum_{s = 1}^{S} I_{ks} \rho_{sk}C_{sk\rightarrow jk},
\]

where \( I_{b0} \) and \( I_{d0} \) are the sources of direct and diffuse radiation on a horizontal plane, \( K \) is the number of vegetation cells, \( \rho_{jk} \) is the scattering coefficient of component \( j \) (i.e. the sum of leaf transmittance and reflectance), \( S \) is the number of soil surface zones, and \( \rho_{sk} \) is soil reflectance. The four terms of the right member of Eqn 5, respectively, account for interception of (i) direct (ii) diffuse, and scattered radiation by (iii) the plant components and (iv) the soil surface. Similar equations are added for fluxes \( I_{s} \) transmitted to each elementary soil surface \( s \) \((s = 1, \ldots, S)\)

\[
I_{s} = I_{b0}C_{b0\rightarrow s} + I_{d0}C_{d0\rightarrow s} + \sum_{k = 1}^{K} \sum_{j = 1}^{J} I_{jk} \rho_{js}C_{jk\rightarrow s}.
\]

Equations 5 & 6 make a linear system of \( \sum_{k = 1}^{K} J(k) + S \) equations, where fluxes \( I_{jk} \) and \( I_{s} \) are the unknowns.

As coefficients \( \rho_{jk} \) and \( \rho_{js} \) depend on wavelength, the system of Eqs 5 & 6 is successively solved for the PAR and NIR wavebands. Finally absorbed radiation by component \( j \) in cell \( k \) is \((1 - \rho_{jk})I_{jk} \).

As the direct beam is intercepted by the only sunlit area, the amount of sunlit and shaded area of component \( j \) in cell \( k \) (denoted \( I_{j}^{\text{sun}} \) and \( I_{j}^{\text{shade}} \), respectively) can be computed from the exchange coefficient \( C_{b0\rightarrow jk} \). Radiation fluxes intercepted by the sunlit and shaded area of component \( j \) in cell \( k \) may be, respectively, written

\[
I_{jk}^{\text{sun}} = I_{bo}G_{jk}(\Omega_{\text{sun}})/\sin h_{\text{sun}} + I_{d0}C_{d0\rightarrow jk}
+ \sum_{k' = 1}^{K} \sum_{j' = 1}^{J} I_{jk'} \rho_{jk'}C_{jk'\rightarrow jk} + \sum_{s = 1}^{S} I_{ks} \rho_{sk}C_{sk\rightarrow jk},
\]

\[
I_{jk}^{\text{shade}} = I_{bo}C_{b0\rightarrow jk} + \sum_{k' = 1}^{K} \sum_{j' = 1}^{J} I_{jk'} \rho_{jk'}C_{jk'\rightarrow jk} + \sum_{s = 1}^{S} I_{ks} \rho_{sk}C_{sk\rightarrow jk},
\]

where \( h_{\text{sun}} \) is sun elevation. Outputs of the solar radiation model are PAR and NIR fluxes intercepted by both sunlit and shaded area of each plant component in each 3D cell.

**Energy budget**

The radiation model has been coupled with an energy balance model. For each 3D cell \( k \), the energy balance of each component \( j \) may be written

\[
Q_{jk} - H_{jk} - E_{jk} = 0.
\]

\( Q_{jk} \) is net radiation, and \( H_{jk} \) and \( E_{jk} \) are sensible and latent heat fluxes. Solving the energy balance amounts to seeking surface temperature balancing gained and lost heat fluxes. The model separates the energy balance of sunlit and shaded area as differences in surface temperatures can be expected because of the energetic effect of direct radiation and the light effect on stomatal control.

The following equations are given for sunlit area only, but similar equations hold for shaded area. Net radiation can be written by splitting the radiation balance according to three wavebands [PAR, NIR and thermal infrared radiation (TIR)]

\[
Q_{jk}^{\text{PAR}} = I_{jk}^{\text{PAR}} + I_{jk}^{\text{NIR}} + I_{jk}^{\text{TIR}} - 2\sigma T_{jk}^{\text{sun}} A_{jk}^{\text{sun}},
\]

where the last term of the right member accounts for emitted radiation. Fluxes \( I_{jk}^{\text{PAR}} \) and \( I_{jk}^{\text{NIR}} \) are given by
Eqn 7, where incident fluxes ($I_{da}$ and $I_{db}$) and optical properties ($\rho_d$ and $\rho_s$) depend on waveband. PAR and NIR are assumed to contribute solar radiation by 48 and 52%, respectively (Varlet-Grancher 1975). Intercepted TIR flux $I_{TR}^j$ is computed according to the same principles as for PAR and NIR (see Eqn 5). However, scattered radiation is neglected because scattering coefficients of soil and leaf surfaces in TIR waveband are close to zero (Monteith & Unsworth 1990). Moreover radiation $M$ emitted by the plant components and the soil surface must be included. This leads to

$$I_{TR}^j = I_{dTR}^j C_{d;jk} + \sum_{k' = 1}^{K} \sum_{j' = 1}^{J} M_{jk'} C_{jk'}^{j' - jk} + \sum_{s = 1}^{S} M_{s} C_{sj - jk}$$  \hspace{1cm} (11)

with $M_{jk} = \frac{A_{jk} \cdot \sigma \cdot T_{jk}^{sun} + A_{jk}^\text{shade} \cdot \sigma \cdot T_{jk}^{shade}}{A_{jk}}$.  \hspace{1cm} (12)

In Eqn 11, $I_{dTR}^j$ accounts for atmospheric radiation. Emitted radiation $M$ only depends on the Stephan–Boltzman constant ($\sigma = 5.67 \times 10^{-8}$ W m$^{-2}$ K$^{-4}$) and surface temperature of both sunlit ($T_{jk}^{sun}$) and shaded ($T_{jk}^{shade}$) foliage area, because leaf and soil surfaces are assumed to be black bodies. Radiation emitted by the soil surface $M_s$ is computed in a similar way. This assumption avoids solving the linear system for TIR.

Sensible heat flux lost by the sunlit area of component $j$ in cell $k$ may be written

$$H_{jk}^{sun} = \rho \cdot c_p \cdot g_b \cdot (T_{jk}^{sun} - T_{jk}^{air}) \cdot A_{jk}^{sun},$$  \hspace{1cm} (13)

where $\rho$, $c_p$, and $g_b$ are air density (kg m$^{-3}$), heat capacity of the air (J kg$^{-1}$ K$^{-1}$) and leaf boundary layer conductance (m s$^{-1}$), respectively. $T_{jk}^{air}$ is air temperature in cell $k$. Conductance $g_b$ is parameterized as a function of local wind speed $U_c$.

Latent heat flux lost by sunlit area of component $j$ in cell $k$ is

$$E_{jk}^{sun} = \frac{\rho \cdot c_p}{\gamma} \cdot g_{sun} \cdot (\varepsilon_{jk}^{sun} - \varepsilon_{jk}^{air}) \cdot A_{jk}^{sun},$$  \hspace{1cm} (14)

where $\gamma$ is the psychrometric constant (Pa K$^{-1}$), $\varepsilon_{jk}^{sun}$ (Pa) the saturated water vapour pressure at temperature $T_{jk}^{sun}$, $\varepsilon_{jk}^{air}$ the water vapour pressure in the air of cell $k$ and $g_{sun}$ the leaf conductance (m s$^{-1}$) for water vapour transfer, which is computed by combining boundary layer and stomatal conductances of both upper and lower leaf surfaces, $g_{sun}^u$ and $g_{sun}^l$

$$g_{sun} = \frac{1}{\frac{1}{g_b} + \frac{1}{g_{sun}^u}} + \frac{1}{\frac{1}{g_b} + \frac{1}{g_{sun}^l}}.$$  \hspace{1cm} (15)

According to Jarvis (1976), non-synergistic interactions between plant and environmental variables controls stomatal conductance. For hypostomatoous leaves, $g_{sun}^u$ (m s$^{-1}$) is computed as

$$g_{sun}^u = g_{sl}^{max} \cdot f_c (\varepsilon_{jk}^{sun} - \varepsilon_{jk}^{air}) \cdot f_{PAR}(I_{sun}^{PAR}) \cdot f_T(T_{jk}^{sun}) \cdot f_{CO_2}(C_k),$$  \hspace{1cm} (16)

where $(\varepsilon_{jk}^{sun} - \varepsilon_{jk}^{air})$ is the air water vapour pressure deficit at the leaf surface (VPD, Pa), $C_k$ is the air CO$_2$ partial pressure at the leaf surface (Pa), and $g_{sl}^{max}$ is the maximum stomatal conductance. In order to account for leaf acclimation to the mean light regime, $g_{sl}^{max}$ can be empirically related to the time-averaged leaf irradiance (Le Roux et al. 1999a)

$$g_{sl}^{max} = a + b \cdot \langle I_{jk}^{PAR} \rangle / \langle I_{s}^{PAR} \rangle$$  \hspace{1cm} (17)

where $\langle I_{s}^{PAR} \rangle$ is time-averaged incident PAR (mol PAR m$^{-2}$ d$^{-1}$).

The energy balances of sunlit and shaded area of each component in each 3D cell make a system of non-linear equations where surface temperature $T_{jk}^{sun}$ and $T_{jk}^{shade}$ are unknown. Non-linearity results from the effect of surface temperature on emitted radiation, saturated water vapour pressure and stomatal conductance. Moreover, energy balance equations are theoretically interdependent because of the exchange of thermal infrared radiation. However, in practice, the energy balance of any sunlit or shaded component is most sensitive to its own surface temperature, so that equations can be solved independently. Each energy balance is therefore solved by using the iterative Newton–Raphson method (Nougier 1985).

Outputs of the energy balance model are finally surface temperature and transpiration fluxes of sunlit and shaded area of each foliage component in each 3D cell.

**Photosynthesis**

Carbon gain is computed for sunlit and shaded leaves of each vegetation component in each 3D cell. Photosynthetic rates are simulated according to Farquhar, von Caemmerer & Berry (1980). The model version proposed by Harley et al. (1992) was used without including the potential limitation arising from triose phosphate utilization. Input variables are leaf irradiance and leaf temperature as computed by the radiation and energy balance models, and air CO$_2$ partial pressure. Net CO$_2$ assimilation rate ($A$, $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$) is expressed as

$$A = [1 - (0.50/(\tau C_i))] \min(W_c, W_t) - R_d$$  \hspace{1cm} (18)

where $W_c$ (\mu mol CO$_2$ m$^{-2}$ s$^{-1}$) is the carboxylation rate limited by the amount, activation state and/or kinetic properties of Rubisco, $W_t$ (\mu mol CO$_2$ m$^{-2}$ s$^{-1}$) is the carboxylation rate limited by the rate of RuP$_2$ regeneration, $\tau$ is the specificity factor for Rubisco, $R_d$ (\mu mol CO$_2$ m$^{-2}$ s$^{-1}$) is the rate of CO$_2$ evolution in light which results from processes other than photorespiration, and $O$ and $C_i$ (Pa) are the partial pressures of O$_2$ and CO$_2$ in the intercellular air spaces, respectively. Rubisco activity is likely to restrict assimilation rates under conditions of high irradiance and low $C_i$. RuP$_2$ regeneration is likely to be limiting at low irradiance and when $C_i$ is high. At a given leaf temperature, the key model parameters (maximum carboxylation rate, maximum electron transport rate, and respiration rate) are linearly related to the amount of nitrogen per unit leaf area (Le Roux et al. 1999a). Leaf nitrogen $N_{jk}$ (g m$^{-2}$) of com-
ponent $j$ in cell $k$ is estimated from mean leaf irradiance ($I_{RPAR}^{(k)}$) (i.e. computed by the radiation model over a 7 d period) by an empirical linear relationship (e.g. Le Roux, Sinoquet & Vandame 1999b)

$$N_{jk} = a + b \cdot N_{0j} \cdot \left(\frac{I_{j_k}^{PAR}}{I_0^{PAR}}\right). \quad (19)$$

where $N_{0j}$ is the amount of nitrogen per unit area of fully sunlit leaves. Equation 19 accounts for the heterogeneity of photosynthetic capacities encountered along light gradients within vegetation canopies (e.g. Ellsworth & Reich 1993; Le Roux et al. 1999b; 2001). In the model, $C_j$ is not explicitly computed, as an analytical solution is used to couple the photosynthesis and stomatal conductance submodels (Wang & Jarvis 1990). All the equations used in the photosynthesis model are given in Le Roux et al. (1999a).

Field measurements on an isolated tree crown

The RATP model was applied to a 20-year-old walnut tree (Juglans regia L.) in a 1-5 ha timber plantation at Plauzat, France (45°N, 2°E). Trees were planted in 1976 at a density of 100 individuals ha$^{-1}$, and were around 7.5 m high. The tree selected for this study was 7-9 m high and was located in the middle of the plot. The tree crown had a maximal diameter of 6-5 m (north–south) and was 5 m high. Measurements in the walnut tree were made in August to September 1996.

Tree architecture and foliage distribution

The tree architecture was measured in September 1996 as reported by Sinoquet, Rivet & Godin (1997). The spatial co-ordinates of the tips of all leafy shoots were measured with an electromagnetic 3D digitizer (Fastrak, Polhemus Inc., Colchester, VT, USA). This device allows spatial co-ordinates of tree organs to be measured with an accuracy <3 cm. In the same time as the digitizing, the basal diameter of the shoots was measured with a Vernier calliper. The leaf area of a sample of shoots was measured with a Li-3100 area meter (LI-COR Inc., Lincoln, NE, USA) in order to derive an allometric relationship between the basal shoot diameter $D_{shoot}$ (mm) and leaf area $A_{shoot}$ (cm$^2$) at shoot scale

$$A_{shoot} = 22.416D_{shoot}^2 - 36.391D_{shoot} \quad r^2 = 0.97 n = 16 \quad (20)$$

This relationship was used to compute the leaf area associated to each shoot in the tree. The tree exhibited 1730 leafy shoots, and its total leaf area was estimated to be 144 m$^2$ for a 95 m$^3$ crown volume (Sinoquet et al. 1997). Further details about the procedure for tree architecture acquisition are given in Sinoquet & Rivet (1997). For model application, the tree crown was divided into 3D cells of 0.5 m $\times$ 0.5 m $\times$ 0.5 m according to mean shoot extension (Fig. 1). Each shoot was allocated to a cell according to its spatial co-ordinates (i.e. 550 cells including foliage). As leaf orientation was not measured, uniform distribution of leaf azimuth and spherical distribution of leaf inclination were assumed.

Spatial distribution of microclimate within the crown

Wind speed, air temperature and air water vapour pressure were measured at 11 locations along vertical and horizontal (north–south) transects, as described by Daudet et al. (1999). Leaflet boundary layer conductance was assessed by heated replicas of walnut leaflets distributed in the tree crown (using the methodology presented by Daudet et al. 1998, 1999). Measurements of microclimatic variables showed the absence of gradient in air temperature or water vapour pressure within the tree crown. Moreover a strong correlation between wind speed attenuation ($U/U_0$, where $U_0$ is incident wind speed) and the total amount of foliage along wind vector ($L_{cum}(\vec{U})$), and between leaflet boundary layer conductance ($g_b$, in mm s$^{-1}$) and local wind speed ($U$, in m s$^{-1}$) was found (Daudet et al. 1999)

$$U/U_0 = 0.952 - 0.07L_{cum}(\vec{U}) \quad r^2 = 0.85 \quad (21)$$

$$g_b = 10U + 71 \quad r^2 = 0.96 \quad (22)$$

For model application, air temperature and water vapour pressure were therefore assumed to be constant within the tree crown, and Eqs 21 & 22 were used to compute the spatial distribution of leaf boundary layer conductance.

Measurement of leaf irradiance for individual shoots

Leaf irradiance in the PAR waveband was measured for five shoots in contrasted locations in the tree: at the bottom ($S_{bottom}$) and the top ($S_{top}$) of the crown, and at middle height in the crown periphery in the east ($S_{East}$), south ($S_{south}$) and west ($S_{West}$) directions. Leaf area of those shoots ranged from 0.08 to 0.28 m$^2$, and the leaflet number was between 27 and 57. Each shoot was equipped with 12 PAR microsensors fixed on randomly sampled leaflets. The sensors were amorphous silicon cells (Solems S.A., Palaiseau, France) coated with transparent thermo-retractable plastic sheath to ensure they were watertight (Adam & Sinoquet 1997). Sensors had a low mass (0.8 g) and were connected with thin wires, so that leaflet orientation was undisturbed. The sensors were calibrated against a commercial quantum sensor (SKP 215, Skye Instruments Ltd, Powys, UK) in the open during a sunny day. The 5 x 12 sensors were connected to one data logger (CR10, Campbell Scientific Ltd, Shepshed, Leics., UK) via five junction boxes and a multiplexer (AM416, Campbell Scientific Ltd). Commercial amorphous silicon cells (PAR-CBE, Solems S.A.) located above the tree canopy were used to measure global and diffuse (i.e. using a shadow band) incident PAR, and were connected to the same data logger. Data of individual sensors were scanned every 15 s and averaged every 15 min. Mean shoot irradiance was estimated as the average of data from the 12 sensors attached to the shoot.
Measurements of transpiration and photosynthesis

Sapflow measured by the technique proposed by Valancogne & Nasr (1993) was used to measure transpiration rates continuously. The sap flow meters were installed on four branches located in contrasted zones in the tree: at the bottom (B-bottom), at the top (B-top), and at middle height in the crown periphery in the east (B-east) and south (B-south) directions. Leaf area of those branches ranged from 0.4 to 2.0 m² and the branch diameter was between 21 and 29 mm. Thermocouples were connected to a data logger scanning and averaging data every 15 s and every 10 min, respectively. At the end of the measuring period, the four branches were harvested for direct determination of their total leaf area (Li–3100, LI-COR Inc.).

Photosynthetic rates were measured for two branches located at the southern edge of the tree using a closed branch bag technique and an infrared gas analyser (LCA-2, ADC Inc., Hoddesdon, Herts, UK). On 22 August 1996, branch photosynthesis was measured alternatively for each branch at different PAR levels between 1200 and 1830 h. The 0.34 m³ branch bag was sealed on the branch with mastic to ensure air-tightness. Incident total and diffuse PAR was measured at 1 min time-steps during the measurement period. Air was continuously pumped from the chamber at a rate of 1.2–1.4 dm³ min⁻¹ and pushed into the analyser after passing through a MgClO₄ water trap. Branch photosynthesis was determined from the depletion rate of CO₂ concentration within a 2–3 min period after closing the chamber. Good linearity of CO₂ depletion with time was observed during all the measurements. On 23 August, all the leaves of each branch were sampled and placed on ice immediately. Fresh leaflet area was measured in the laboratory with a Li-cor area meter. Then, leaflets were frozen in liquid nitrogen and lyophilized, and their dry mass was measured. Total nitrogen concentration of each leaf sample was determined from elemental analysis (CHNS-O, EA1108, Carlo Erba Instruments, Milan, Italy).

For model application, the set of shoots downstream of the sapflow meter location or included in the branch bags was defined as a vegetation component. The tree was thus split into five vegetation components (four branches equipped with the sapflow meters plus the rest of tree foliage) and three vegetation components (two branch bags plus the rest of tree foliage) for transpiration and photosynthesis simulations, respectively.

Spatial distribution of leaf properties

The optical properties of leaves and soil were measured using a Li-cor 1800 spectrophotometer. Leaf absorptance was 0.83 and 0.13 in the PAR and NIR wavebands, respectively. Optical leaf properties remained almost constant along light gradients within the tree crown (Combes, Sinoquet & Varlet-Grancher 2000). Soil reflectance was 0.07 and 0.20 in PAR and NIR wavebands, respectively.

The spatial distribution of leaf nitrogen was computed from an empirical relationship with leaf irradiance averaged over a 1-week-period (Le Roux et al. 1999b). The stomatal response to PAR at ambient CO₂ partial pressure (35 Pa) was measured on leaves of a 2-year-old walnut tree in standard conditions (air temperature = 25 °C, VPD = 1000 Pa). The relative stomatal conductance (i.e. ratioed to that measured at 1500 µmol PAR m⁻² s⁻¹) was closely related to leaf PAR irradiance (Fig. 2). Function F(par) in Eqn 16 was fitted to the data as a second-order polynomial. Other stomatal responses included in Jarvis’ model (i.e. responses to VPD, leaf temperature and CO₂ concentration, and effect of mean radiation regime on maximum stomatal conductance) and the photosynthesis model of Farquhar et al. (1980) (relationships between photosynthetic capacities and N) were parameterized for leaves in different locations within the adult tree crown (Le Roux et al. 1999a). The temperature dependence of the key model parameters is given in Le Roux et al. (1999a).

RESULTS

Values of the main parameters and ranges of driving variables used in the simulation runs are given in Table 1.

Simulation of the leaf radiation regime at shoot scale

Figure 3 shows the time course of irradiance measured on sunlit leaflets during a sunny day (18 August 1996). The micro-sensor data matched a simple relationship giving the irradiance of sunlit tilted surface as a function of surface orientation (inclination α, azimuth φ), sun direction and the
amount of incident direct and diffuse radiation \( (I_{b0} \text{ and } I_{d0}) \) (Varlet-Grancher 1975)
\[
I_{ap} = I_{b0} \max[\cos \beta, 0] + I_{d0} \cos^2(\alpha/2)
\]  
(23)

where \( \beta \) is the angle between surface normal and the sun direction. Data were correctly simulated by Eqn 23 when the sensor received only diffuse radiation (\( \cos \beta < 0 \), e.g. sensor no.32 in the morning) or both direct and diffuse incident radiation. When sensors were sunlit during the whole day (e.g. sensor no.26 and no.32), \( r^2 \) coefficients between measured data and Eqn 23 were around 0·98. Moreover the diurnal courses of mean shoot irradiance (i.e. average of 12 leaflet irradiance) during two similar days (i.e. similar time course of direct and diffuse incident radiation) were not significantly different (slope = 1·00, \( r^2 = 0·99 \)) (data not shown). These results suggest that light microsensors provided correct estimations of leaf irradiance.

For each sampled shoot in the crown, the heterogeneity in leaflet irradiance was very high (Fig. 4). This was because both shaded and sunlit leaflets were encountered on a given shoot at a given time. Leaflet irradiance ranged between less than 100 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for shaded leaflets up to more than 1000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for sunlit leaflets. In addition, shoots which were not in full sunlight experienced sunflecks (e.g. \( S_{\text{Bottom}} \)). In this case, actual leaflet irradiance was below 100 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for a fraction of the total shoot leaf area, whereas other parts of the foliage experienced irradiance values higher than 500 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). Standard error in measured shoot irradiance therefore ranged from 5 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) in shaded zones to 180 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) in sunlit areas.

The RATP model adequately simulated the magnitude and the daily course of mean leaf irradiance at shoot scale (Fig. 4). In particular, the model was able to simulate transient increases in shoot irradiance related to canopy gaps (e.g. \( S_{\text{Bottom}} \)). Root mean square error of prediction...
(RMSEP) ranged from 60 (SBottom) to 120 µmol m$^{-2}$ s$^{-1}$ (STop). When considering all shoots together, RMSEP of shoot irradiance was 90 µmol m$^{-2}$ s$^{-1}$. However, the model slightly overestimated mean shoot irradiance, as the mean deviation between simulated and measured values was +40 µmol m$^{-2}$ s$^{-1}$. Comparison at daily scale confirmed the model overestimation of shoot irradiance which showed a RMSEP of 2.1 mol m$^{-2}$ s$^{-1}$ and a mean deviation of +1.7 mol m$^{-2}$ day$^{-1}$ (Fig. 5).

**Simulation of transpiration for individual shoots**

Figure 6 shows the diurnal course of transpiration rates of branches BBottom, BEast and BSouth during a sunny day (24 August 1996). The observed maximum transpiration rates per unit leaf area ranged from 0.95 g m$^{-2}$ min$^{-1}$ for BBottom, up to 2.2 g m$^{-2}$ min$^{-1}$ for BSouth (Fig. 6). Furthermore, maximum sap flow rates were observed around 13 h for BEast, whereas maximum values were obtained around 15 h for BBottom and BSouth.

The diurnal course of branch transpiration rates simulated by the RATP model showed a satisfactory agreement with measurements (Fig. 6). In particular, the model properly accounted for the differences in the magnitude of transpiration rates which arose from location of each branch in the tree crown. Differences in time of maximal transpiration rate according to spatial location were also captured by the model. When considering all branches together, the relationship between simulated and observed values of transpiration rates at branch scale was linear and unbiased (Fig. 7). Regression analysis showed a slope not significantly different from 1 and an $r^2$ coefficient of 0.83. RMSEP was 0.25 g m$^{-2}$ min$^{-1}$, i.e. about 10% of maximal transpiration rate, whereas the mean deviation was –0.10 g m$^{-2}$ min$^{-1}$.

RMSEP computed for individual branches ranged from 0.13 to 0.31 g m$^{-2}$ min$^{-1}$ for BBottom and BEast, respectively. Model bias was almost zero for BBottom and BTop, whereas it reached the maximum value of –0.25 g m$^{-2}$ min$^{-1}$ for BEast.

**Simulation of photosynthesis for individual shoots**

The simulated values of leaf nitrogen (see Eqn 19) for the two branches studied (2.51 and 2.17 g m$^{-2}$) was close to
observed data for these branches (2·48 and 2·33 g m⁻²). Concurrently, the values of photosynthetic rates at branch scale simulated by RATP on 22 August 1996 were in good agreement with the observed values (Fig. 8). RMSEP including all points was 1·9 m mol CO₂ m⁻² s⁻¹, i.e. about 12% of maximal assimilation rate. The model better simulated carbon gains below 12 m mol CO₂ m⁻² s⁻¹ (RMSEP = 0·8 m mol CO₂ m⁻² s⁻¹), whereas the error was greater for higher assimilation rates (RMSEP = 2·5 m mol CO₂ m⁻² s⁻¹, and the model underestimated A).

**DISCUSSION**

The model RATP was designed to simulate the spatial distribution of carbon gain and water loss within canopies as a function of the spatial distribution of leaf area, distinguishing several foliage components. Those features provide the model with a large range of applications. On one hand, the model can be applied to a range of vegetation canopies exhibiting contrasting geometry, e.g. from grasslands to forests. On the other hand, the model can be used to study resource partitioning between vegetation components, e.g. species in intercropping, agroforestry or savanna systems (Simioni et al. 2000), weeds and crops, individuals in heterogeneous canopies, and organs within a plant, as illustrated by the present application to an isolated walnut tree at shoot and branch scales. Other models have been proposed, which could be used to deal with the spatial distribution of plant function. Most of them focus on light microclimate (Myneni 1991; Gastellu-Etchegorry et al. 1996) and/or may include leaf photosynthesis responses (Myneni 1991; Chen et al. 1994; Desmarez et al. 2000). The model MAESTRO (Wang & Jarvis 1990; Kruijt et al. 1999) also includes transpiration within tree crowns. These models have been mainly used to scale up from the leaf to the canopy, i.e. to compute properties or fluxes at the canopy scale and that is probably the reason why they have not been tested at intracanopy scale. In this study, we attempted to test the RATP model at a shoot or branch scale, i.e. a fine intracanopy scale; indeed, the maximum leaf area on a shoot sampled for light capture and by a branch equipped with a sapflow meter was 0·28 and 2·0 m², i.e. 0·2 and 1·4% of the whole tree foliage, respectively.

The main hypotheses used in the model RATP are the turbid medium analogy for radiation computations, and the use of several empirical relationships for the plant responses. The most critical assumption of the turbid medium analogy is the random leaf dispersion, i.e. leaves are assumed to be randomly located in space (Nilson 1971). This assumption is commonly violated in real canopies, especially in trees which usually show foliage clumpiness (e.g. Sampson & Smith 1993). As warned by Cohen, Mosoni


![Figure 5](image.png)

**Figure 5.** Relationship between the daily shoot irradiance measured in the field PAR_{mes} and simulated by the RATP model PAR_{sim} on 17 August 1996. Results are presented for five shoots in different locations in the tree crown (see text). Bars are the standard errors of measured shoot irradiance.

![Figure 6](image.png)

**Figure 6.** Comparison of the diurnal course of transpiration rate T measured at branch scale (symbols) and simulated by the RATP model (lines) on 24 August 1996. Results are presented for four branches in different locations in the tree crown.
& Meron (1995), clumpiness and its spatial variations would be critical for models attempting to map radiation fields inside the canopy. Representing the canopy structure as an array of 3D cells filled with turbid medium is a common way to take into account canopy clumpiness resulting from the spatial variations in leaf area density (e.g. Whitehead, Grace & Godfrey 1990). However deviation from the random leaf dispersion may still occur at the cell scale (e.g. Fukai & Loomis 1976). Moreover canopy discretization into 3D cells questions the cell size. As Beer’s law is a negative exponential function, decreasing the cell size leads to lower computed light interception and thus simulates an increased canopy clumpiness. This suggests that cell size could be regarded as a clumping index. As previously pointed out by Nilson (1971), clumping parameters are probably related to structural or botanical features of the plants. However, when taken into account, clumpiness is still always used as a calibration parameter. In this study, cell size (0·5 m) was chosen according to mean shoot extension. As simulated shoot irradiance was overestimated, the actual clumping in the walnut tree was higher than accounted for by the canopy discretization.

With regard to plant responses, most of them – namely the response of leaf boundary layer conductance, stomatal conductance and photosynthesis to current environmental variables, and light acclimation of maximal stomatal conductance and leaf photosynthetic capacity – were simulated from empirical relationships. This is because our knowledge of these processes and their formalization through simple and robust models is rather weak. Sensitivity analyses are needed to evaluate the effect of the parameters of the empirical models. In the case of the RATP model, Daudet et al. (1999) showed that the transpiration rate of the walnut tree exhibited a large sensitivity to the maximal stomatal conductance $g_{\text{max}}$ and a low sensitivity to boundary layer conductance. This results from the high coupling between the plant and the atmosphere, i.e. a usual feature in tree canopies (Infante, Rambal & Joffre 1997; Wullschleger, Wilson & Hanson 2000) resulting from the relative magnitude between stomatal and leaf boundary layer conductances (see McNaughton & Jarvis 1983). Other canopies such as grass stands are highly decoupled from the atmosphere (McNaughton & Jarvis 1983), so that such a sensitivity analysis would lead to opposite conclusions. This means that sensitivity analyses should depend on the application of the model. In case of the walnut tree, other sensitivity analyses are in progress, especially with regard to light acclimation of leaf characteristics within the tree.

Other processes included in the RATP model – namely energy balance and photosynthesis – do not involve special hypotheses. Transpiration is computed from a complete energy balance without assumption on leaf temperature and by distinguishing sunny and shaded leaf area. On one hand, this allows the computation of leaf temperature which may have a major effect on various plant responses (e.g. photosynthesis, Jordan & Ogren 1984; isoprene emission, Zimmer et al. 2000). On the other hand, separating sunlit and shaded areas is an adequate way to deal with the non-linear light response of the energy balance (De Pury & Farquhar 1997; Wang & Leuning 1998). Photosynthesis is computed after the model of Farquhar et al. (1980), which is recognized as simple, efficient and robust by an increasing number of users. However, application of RATP to another species would request to use an adequate parameterization (i) for light acclimation (e.g. Le Roux et al. 2001), and (ii) for temperature dependence of photosynthetic capacity (Dreyer et al. 2001). Moreover modelling both energy balance and photosynthesis depends on stomatal
conductance, for which our understanding is still relatively poor.

RATP does not simulate the canopy microclimate within the canopy, except radiation and, to a lesser extent, wind speed from an empirical relationship (Daudet et al. 1999). Most models aimed at studying tree function do the same (Cohen et al. 1987; Wang & Jarvis 1990). Fortunately, in a number of cases, air characteristics (i.e. wind speed, temperature, humidity) do not show large spatial variations, and/or these spatial variations do not have large effects on CO₂ and H₂O exchanges between the plants and the atmosphere. This was the case for the isolated walnut tree used in this study (Daudet et al. 1999). However, disregarding the effects of plant function on air characteristics prevents us from simulating plant exchanges in contrasting growing conditions (e.g. according to tree density, Green, Grace & Hutchings 1995), except if microclimate variables are measured within each canopy.

In conclusion, the model RATP is primarily a research tool, the purpose of which is to study water and carbon exchanges at the interface between the plants and the atmosphere. Comparisons between measured and simulated values of leaf irradiance, transpiration and photosynthetic rates at shoot or branch scales have shown the proper behaviour of the model. Sensitivity analyses should be used to quantify the weight of parameters and variables involved in plant function (e.g. Daudet et al. 1999), to test simplified assumptions (e.g. Sinoquet & Le Roux 2000), and to derive summary models. The RATP model will be also used to test the optimization theories of plant function (e.g. Hollinger 1996).

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