Scaling leaf photosynthesis to canopy in a mixed deciduous forest. I. model description

SAMSON, R., FOLLENS, S. & LEMEUR, R.

Laboratory of Plant Ecology, University of Ghent, Coupure links 653, b-9000 Ghent, Belgium
e-mail: roeland.samson@rug.ac.be

Abstract

A multi-layer model (FORUG) was developped, to simulate the canopy photosynthesis of a mixed deciduous forest during the growing season. Measured photosynthesis parameters, for beech (*Fagus sylvatica*), oak (*Quercus robur*) and ash (*Fraxinus excelsior*), were used as input to the model. This information at the leaf level is then scaled up to the level of the canopy, taking into account the radiation profiles (diffuse and direct PAR) in the canopy, the vertical LAI distribution, the evolution of the LAI and the photosynthesis parameters during the growing season, and the temperature dependence of the latter parameters.

***Key words** : multi-layer model, photosynthesis, scaling, mixed deciduous forest, Quercus robur, Fagus sylvatica, Fraxinus excelsior*

1. Introduction

Forests are complex ecosystems, excerting a very important role in several biogeochemical cycles. The carbon, nitrogen and water cycles of a forest are tightly linked (Baldocchi & Harley 1995). As a consequence a major focus of contemporary ecological research is on understanding how carbon, water and nutrient cycles of forest ecosystems respond to environmental and climatic perturbations (Dixon et al. 1990; Agren et al. 1991; Running & Hunt 1993; McMurtrie & Wang 1993). Integrating and synthesising this physiological information across difference scales of organisation can be best done using simulation models.

Particularly in the context of global change, in which plant communities will be subject to hitherto unfamiliar combinations of environmental inputs, the empirical database is necessarily small and predictions of responses at whole-plant and ecosystem scales will increasingly rely on simulation models of the system in question (Harley & Baldocchi 1995). Moreover these authors state that any but the very simplest canopy models should incorporate variation in leaf physiological and/or morphological properties with leaf position in the canopy (Harley & Baldocchi 1995).

For modelling canopy processes one can use big-leaf models or multi-layer models. The former considers the canopy as being one big leaf. This kind of model is rather simple and requires a limited number of input data. Because of this (over)simplification errors are likely to occur, e.g. de Pury & Farquhar (1997) report that such models overestimate rates of photosynthesis. On the other hand models that treat the canopy in terms of a number of layers - multi-layer models - generally avoid these errors (de Pury & Farquhar 1997).

Because the role of CO_2 in global change, and the role of forest in the global carbon cycle, modelling the carbon cycle in forests is of the utmost importance. Understanding the processes of CO_2 fixation and release, can be an important tool for orientating forest policy. Afforestation as a solution for global change is dependent on forest policy making forests act like CO_2 sources or sinks.

An important process in the exchange of CO_2 between the forest and the atmosphere is photosynthesis. The objective of this paper is to describe a one dimensional, multi-layer canopy photosynthesis model (FORUG model) for application in deciduous forests, consisting of different tree species.The aim is to use the model in actual and future (global change) climatic conditions. The model has as an input climatological parameters, stand parameters (vertical leaf area profile) and ecophysiological parameters (extinction coefficients and gas-exchange parameters). Variation in leaf physiological properties with leaf position in the canopy is taken into account.

2. Material and methods

2.1. Site

Physiological and meteorological measurements were made during the growing seasons 1996 and 1997 in a mixed deciduous forest. The two main forest types are an oak-beech forest, with *Quercus robur* L. and *Fagus sylvatica* L. as dominating trees, and and ash forest type, with *Fraxinus excelsior* L. as the dominant tree. The dominating trees of both forest types are all about 70 years old. The field site is located in East-Flanders (Belgium) (latitude 50°58'35" N; longitude 3°49'30"; elevation between 11 and 21 m above sea level). The canopy height was around 27 m, and a 35 m high measuring tower provide access to leaves of beech (at 7, 14 and 21 m) and ash (at 21 m). Maximum leaf area index of the oak-beach and the ash forest type during the 1996 growing season were respectively 5.52 and 4.53 m^2 m^{-2}. In the following text the canopy heights 7, 14 and 21m will be translated as Layer 1, Layer 2 and Layer 3. More information about the site and the experimental set-up can be found in Samson et al. (1996).

2.2. Field and laboratory measurements

2.2.1. Gas exchange measurements

A branch, from a particular level in the canopy, was excised. After the branch was brought down the tower, it was recut under water (a shortening by 15 cm)(Wang 1996), and brought to the laboratory. Rates of leaf photosynthesis were measured in the controled environment (T_{air} 20°C and 78% RH) of the phytotron (Figure 1). These two values are mean values for the months May until October calculated from meteorological records of the RMI for the period 1984-1993 (meteorological station Kruishoutem). CO_2 gas exchange rates of the leaves were analysed using an IRGA (225-MK3, ADC) in differential mode. The measurements were begun at a high level of photon flux density, which was then decreased in steps, allowing sufficient time for the steady-state rates of gas-exchange to be attained (0.5-1 h). The measurements were concentrated in August and September 1996. The gas-exchange parameters were calculated using a negative exponential equation according to Goudriaan (1982).

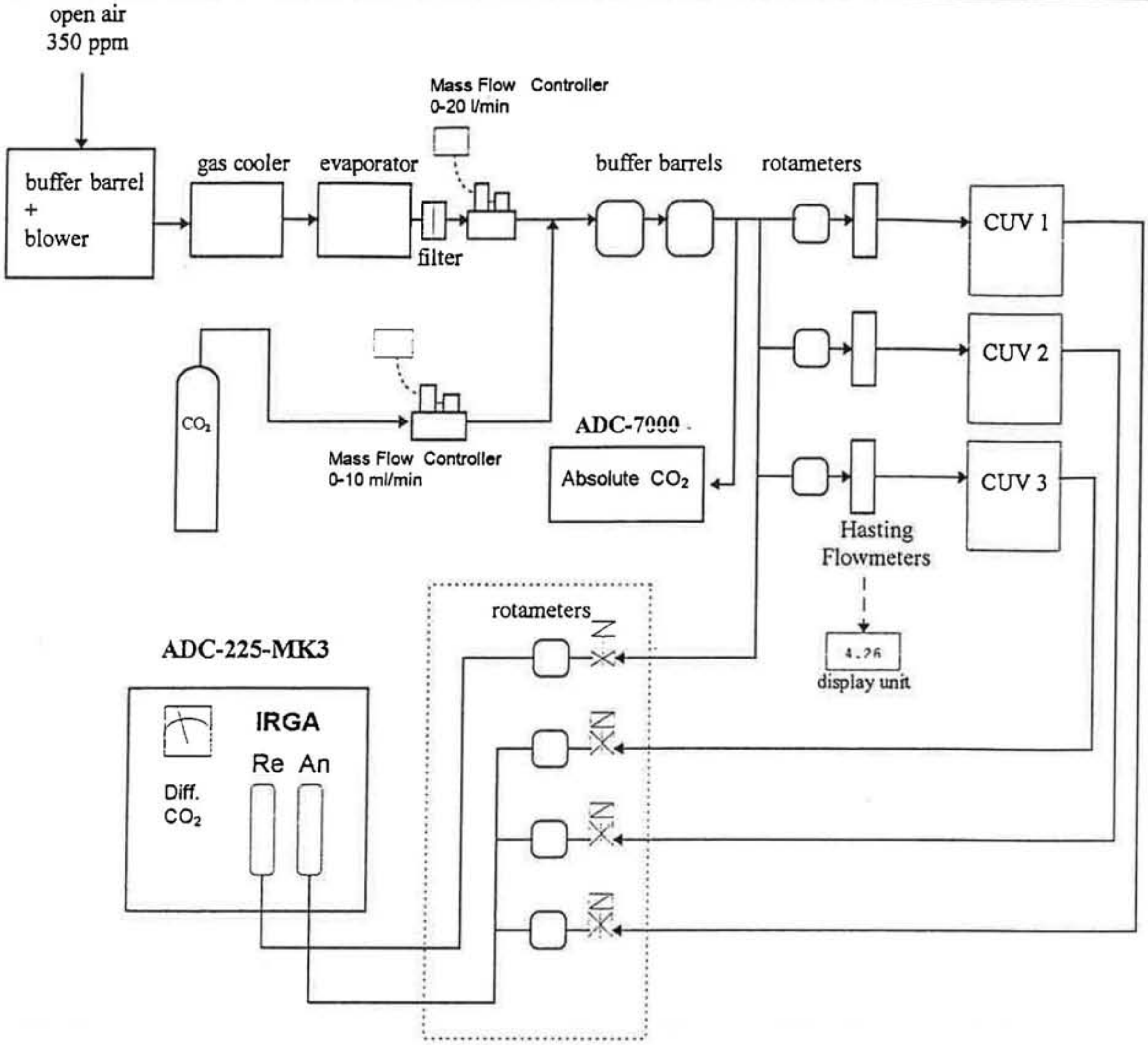

Figure 1. Schematic overview of the phytotron of the Laboratory of Plant Ecology used to measure the CO_2 gas exchange of leaves

2.2.2. Vertical distribution of the leaf area and extinction coefficients

During the 1996 growing season leaf area index (LAI) and photosynthetic active radiation (PAR) photon flux density (PPFD) were measured at different levels in the canopy (7, 14, 21 m). Combining these two measurements yielded the vertical LAI distribution in the canopy besides extinction coefficients.

The leaf area profile through the canopy (0, 7, 14, 21 m) was approximated using a leaf area sensor (LAI-2000, LI-COR). A view cap of 180° was selected. Measurements were made under egal cloudy conditions (September 19). For calibration of this optical, indirect method, also a direct method was used. In both forest type 30 litter traps of 1 m^2 each were installed. Collecting, on a fortnightly basis, leaf litter fall from mid August untill all leaves had fallen, yielded the maximum leaf area index during the 1996 growing season. These absolute values were used for the correction of the total cumulative LAI values obtained with the LAI-sensor.

The PPFD-profile in and under the canopy was measured using the Sunfleck ceptometer (SF-80, Delta-T Devices). This linear sensor excist of 80 quantum sensors, spaced one centimeter from each other. A mean value for these 80 sensors was recorded in the memory of the device. Measurements were done during a sunny day (July 21)(maximal direct radiation) and a cloudy day (August 12)(only diffuse radiation). Above the canopy the PAR intensity was measured using a quantumsensor (SKYE, type SKP 215) connected to an integrator (MV2, Delta-T Devices). In the canopy, the PPFD intensity was measured at the middle of the east, west and north side on each level of the measuring tower. On every place several measurements were executed making a half circular movement with the ceptometer. A measurement was also made one meter above soil level. Every hour this procedure was repeated.

Extinction coefficients are calculated from the two latter parameters, namely PPFD and the cumulative LAI values at different depths in the canopy (Baldocchi & Hutchison 1986). For both parameters, PPFD-profile and vertical LAI-distribution, the measurements on each respective level were averaged, and these mean values were used in the calculations.

The radiation profile within a canopy can be approximated by an exponential relationship (Baldocchi et al. 1984). This relationship is generaly expressed as a form of the Beer-Bouguer Law:

$$I\,(f) = I_o \exp\,(-kf)$$

where $I\,(f)$ is the flux density of a given radiation component below a cumulative plant area (or leaf area) index f, I_o is the radiation flux density incident upon the canopy, and k is the extinction component for the radiation component of interest (here PAR-radiation). This equation can be represented graphically by plotting $\ln(I/I_o)$ against f.

3. Results

3.1. Leaf photosynthesis

Leaf morphology and physiology are likely to change in a continuous manner with reductions in PPFD with depth in a tree canopy (Sellers et al. 1992). Hence the discrete terms 'sun-acclimated' and 'shade-acclimated' leaves can be employed here to distinguish between leaves of beech growing at the top of the canopy (21m) and those found at the lower depths (14 and 7 m). The two groups of leaves are morphologically distinct. This was shown by large differences in specific leaf area (SLA; area/mass) (Table 1). For ash and oak the difference in SLA for sun-acclimated and shade-acclimated leaves was not examined, as their canopies are only accessible at the top of the forest (21m).

Table 1. The SLA of beech, at different height in the canopies (n=8, and each sample was a mean of 5 randomly chosen leaves)

[a] significantly different at P=0.01

[b] significantly different at P=0.05

	SLA±SE ($m^2\ g^{-1}$)	Range ($m^2\ g^{-1}$)
Layer 1	$0.0271 \pm 0.0016^{a,b}$	0.0230-0.0332
Layer 2	$0.0228 \pm 0.0002^{a,b}$	0.0214-0.0235
Layer 3	0.0143 ± 0.0001^{a}	0.0138-0.0149

A summary of the leaf photosynthesis parameters is given in Table 2, for all three species. Beech has a maximal CO_2 exchange rate half of the rates measured for oak and ash. The reaction on an increase in temperature (from 20 to 25 °C) is different for beech and oak. A sharp decline is observed in the net maximal photosynthetic rate of beech, mainly due to a higher respiration rate. For oak a higher net maximal photosynthesis rate is measured, indicating a higher temperature optimum for oak than for beech.

Table 2. Leaf photosynthesis parameters and their respective standard errors for beech (Fagus sylvatica), oak (Quercus robur) and ash (Fraxinus excelsior) measured at two different temperatures. Measurements were excecuted at 350 ppm CO_2 *and 78% RH. (*α*=initial quantumefficiency in µmol* CO_2 *µmol*$^{-1}$ *PPFD;* P_{max}*=maximal gross photosynthesis in µmol* CO_2 m^{-2} s^{-1}*;* R_d*=rate of dark respiration in µmol* CO_2 m^{-2} s^{-1}*)*

	T (°C)	α	P_{max}	R_d
beech (layer 1)	20	0.088±0.004	5.47±0.17	0.31±0.06
	25	0.071±0.003	3.94±0.13	0.47±0.04
beech (layer 2)	20	0.094±0.004	5.67±0.46	0.26±0.02
	25	0.083±0.005	4.70±0.41	0.41±0.03
beech (layer 3)	20	0.071±0.008	5.79±0.49	0.40±0.04
	25	0.084±0.006	5.32±0.24	0.51±0.04
oak	20	0.076±0.008	11.07±1.97	1.09±0.09
	25	0.070±0.010	12.57±0.63	0.98±0.08
ash	20	0.110±0.007	11.88±1.03	1.38±0.16

3.2. Vertical distributions of the leaf area

Annual cumulative leaf area indices, estimated from integrated leaf litter fall for both forest types during the 1996 growing season, were combined with forestry data (stem number per ha, crown radii) and resulted in leaf area indices for uniform forests of the considered species (Table 3). Measurements of the PAR-profile in the canopies resulted in the relative leaf area for each of the three considered layers and for each species. The resulting LAI for each species and for each layer is given in Table 3. As for ash and oak the LAI in layer 1 is very low, it is assumed that the canopies of the respective tree species only consists of two layers (Layer 2 and 3). The LAI found in Layer 1 for ash and oak is added to Layer 2.

Table 3. Total leaf area (m^2 m^{-2}) and its vertical distribution for the three considered layers for ash, oak and beech used as input for the model. Values between ( ) are corrected

	Layer 1	Layer 2	Layer 3	Total
ash	0.17 (0.00)	1.10 (1.27)	1.22	2.49
oak	0.08 (0.00)	3.07 (3.15)	1.22	4.37
beech	1.05	1.07	3.75	5.87
mean	0.35	1.83	2.06	4.24

For the three considered species the growing season is thought to begin at May 1 and to end at November 30. From July 1 untill September 15, the LAI is maximal. Before and after this period the increase respectively the decrease in LAI behaves linearly. The relative LAI-evolution during the growing season is illustrated in Figure 2. It is important to note that the LAI as such does not necesseraly indicate any physiological activity.

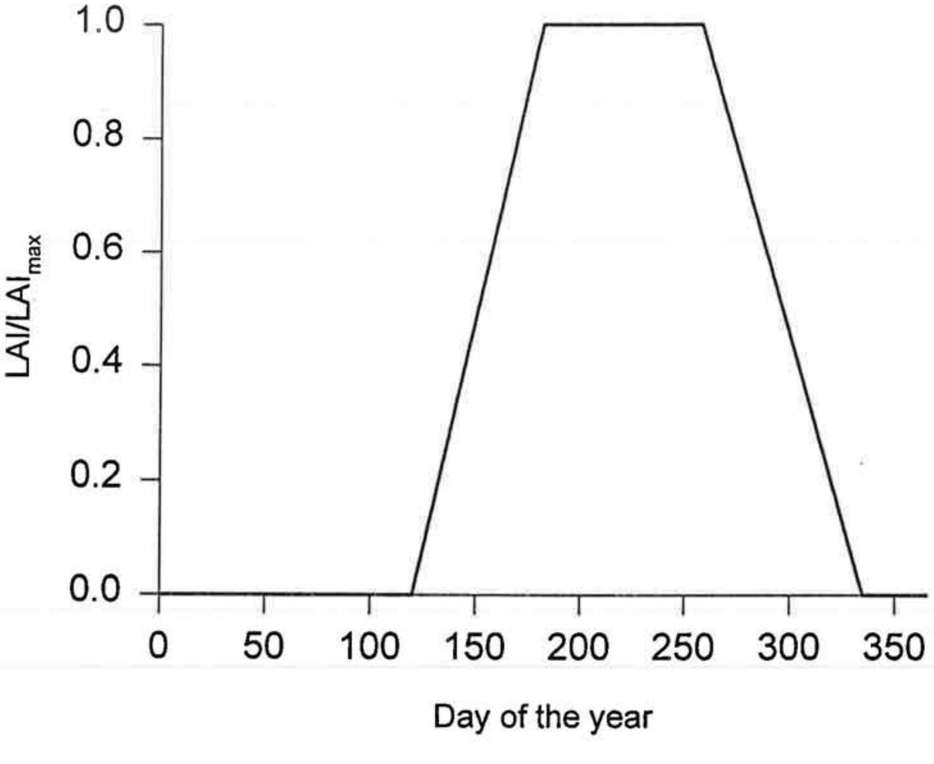

Figure 2. The relative LAI-evolution (-) during the growing season

3.3. Extinction coefficients

From the obtained graphs (not shown here) it is clear that the Beer-Bouguer formula describes the PAR environment reasonably well because the coefficients of determination are large ($r^2 \geq 0.85$).

For the cloudy day (only diffuse radiation) no daily trend is observed in relation to solar elevation, so that a mean extinction coefficient (0.70) for diffuse radiation can be proposed. For the sunny day (only direct radiation), a complex daily pattern is found (Table 4). At low solar elevation the extinction coefficient is relatively low, increasing for somewhat higher solar elevations, while for solar elevations between 40° and 50° again lower values are observed. For solar elevations above 50°the extinction coefficient goes up again. The extinction coefficient for diffuse radiation is lower than the general extinction coefficient measured for direct radiation.

3.4. Model description

Hourly means of the air temperature and incoming shortwave radiation are the meteorological input data to the FORUG-model. Other input data are the leaf photosynthesis parameters, the vertical distribution of the leaf area, and extinction coefficients for diffuse and direct PAR. The output is the hourly net photosynthesis C-uptake or the cumulative net photosynthesis C-uptake for the stand during a defined period. The C-uptake for the considered tree species (beech, oak and ash) and canopy layers (Layer 1, 2 and 3) can be calculated seperatly.

In the three canopy layers, horizontal homogenity is considered, and leaves are behaving as black bodies.

Optimal water and nutrient supplies were assumed.

3.4.1 Submodel solar elevation

In this submodel the hourly position of the sun is calculated during the day. Inputs are the hour of simulation and the latitude of the forest.

The solar elevation is calculated as:

$$\sin\beta = \sin\lambda \sin\delta + \cos\lambda \cos\delta \cos \mathrm{h} \qquad (1)$$

with β solar elevation (°), λ latitude (°) and *h* the hour angle (°).

$$h = 15(t - 0.5 - t_o) \qquad (2)$$

with t the time of the day (h), and t_o the time of solar noon (h). The factor 0.5 in Eq. 2 accounts for the fact that the used meteorological data are hourly means. A certain value measured at e.g. 15h00 represents a mean value between 14h00 and 15h00. In this example the mean value corresponds to 14h30 and not to 15h00.

The solar noon is calculated as:

$$t_o = 12 + \left[4(L_s - L_e) - E_t\right] / 60 \qquad (3)$$

with L_s the standard longitude of the time zone (°), L_e the local longitude (°), and E_t the equation of time in minutes. Note that Eq. 3 only holds for longitudes measured east of Greenwich (Iqbal, 1983).

Different empirical equations exist describing the equation of time. The difference between them is negligible, so the most simple formula is chosen (Woolf, 1968):

$$E_t = 0.258\cos\Gamma - 7.416\sin\Gamma - 3.648\cos 2\Gamma - 9.228\sin 2\Gamma \qquad (4)$$

where

$$\Gamma = \frac{360}{365.242}(D_n - 1) \qquad (5)$$

The declination δ (°) for a given day can be calculated using the model of Cooper (1969):

$$\delta = 23.5\sin\left[\frac{360(D_n + 284)}{365.25}\right] \qquad (6)$$

with D_n the day number.

According to Burman and Pochop (1994), Eq. (6) yields accurate results during the growing season. In October the error is more than 1 degree.

3.4.2. Submodel diffuse and direct incident shortwave radiation

In this submodel the incident shortwave radiation is divided into a direct and diffuse component. Inputs are the daily declination, the latitude, the day of the year D_n and the hourly solar elevation. The output is the variable *D*, describing the hourly portion of the diffuse and direct part in the shortwave radiation. The method used is described in Spitters et al. (1986).

At first the extra-terrestrial solar radiation is calculated according to Sellers (1965):

$$R_{a,d} = \frac{SC}{\pi}\left[\frac{\bar{d}}{d}\right]^2\left[h_s\left\{\frac{\pi}{180}\right\}\sin\lambda\sin\delta+\cos\lambda\cos\delta\sin h_s\right] \qquad (7)$$

with SC :the solar constant (1370 J m^{-2} s^{-1})(Frolich 1982);

$\left[\frac{\bar{d}}{d}\right]^2$:correction for the sun-earth distance; and

h_s :hour angle at sunrise (=-arcos(-tanδtanλ)(°).

According to Duffie and Beckman (1980), the correction for the variation in the sun-earth distance can be simply calculated as:

$$\left[\frac{\bar{d}}{d}\right]^2 = 1 + 0.034\cos\left[\frac{360 D_n}{365.25}\right] \qquad (8)$$

In a second phase the daily atmospheric transmittance of the solar radiattion is calculated. The atmospheric transmittance is the ratio of the incoming solar radiation (at surface of the earth) to the extra-terrestrial radiation ($R_{s,d}/R_{a,d}$). The subscript *d* refers to daily values. The daily incoming solar radiation is measured at the measuring tower. The atmospheric transmittance is supposed to be constant over the day, so that can be written:

$$\frac{R_{s,d}}{R_{a,d}} = \frac{R_s}{R_a} \tag{9}$$

with R_s and R_a respectively the hourly shortwave radiation on the surface of the earth, and the hourly extra-terrestrial radiation. The portion of diffuse radiation in R_s can be represented as *D*, and this parameter is, according to de Jong (1980), in relation to the atmospheric transimittance:

$$\begin{aligned} &D = 1 && \text{if } R_s / R_a \leq 0.22 \\ &D = 1\text{-}6.4(R_s / R_a - 0.22)^2 && \text{if } 0.22 < R_s / R_a \leq 0.35 \\ &D = 1.47\text{-}1.66(R_s / R_a) && \text{if } 0.35 < R_s / R_a \leq P \\ &D = N && \text{if } P < R_s / R_a \end{aligned} \tag{10}$$

with,

$$N = 0.847 - 1.61\sin\beta + 1.04\sin^2\beta \tag{11}$$

$$P = (1.47 - N) / 1.66 \tag{12}$$

3.4.3. Submodel diffuse and direct incoming PAR

In this submodel the incoming PAR is divided into a diffuse and a direct component. As an input the variable *D* is used, together with the hourly shortwave radiation. The output is the diffuse and direct PAR. The method of Ross (1976), also used by Baldocchi and Hutchison (1986), is applied to calculate $I_{PAR,s}$. Hereby it is accepted that the portion of PAR in the direct shortwave radiation is constant, namely 43%:

$$I_{PAR,s} = 0.43R_s(1 - D) \tag{13}$$

$$I_{PAR,d} = R_s(0.07 + 0.43D) \tag{14}$$

with $I_{PAR,s}$ and $I_{PAR,d}$ (J m^{-2} s^{-1}) the direct and diffuse PAR respectively, R_s (J m^{-2} s^{-1}) the total shortwave radiation and *D* the portion diffuse shortwave radiation. The diffuse PAR intensity is then calculated as the difference between the total PAR intensity and the direct PAR intensity. Therefore it is assumed that the fraction PAR in the total shortwave radiation amounts 0.5. This fraction is relative constant over different atmospheric conditions and solar elevation, provided that β is > 10° (Szeicz, 1974). From here on the subscript *PAR* will be omitted. The conversion factor between J m^{-2} s^{-1} and µmol m^{-2} s^{-1} is 4.61 µmol J^{-1}.

3.4.4. Submodel extinction coefficient

In this submodel the extinction coefficient for the direct PAR fraction K_s is calculated as a function of the solar elevation, which is the only input parameter. The extinction coefficient for the diffuse PAR fraction K_d (0.70) is independent for variations in the solar elevation (see 3.3.).
The dependence of K_s in function of the solar elevation is given in Table 4. The extinction coefficient for direct radiation is a discrete value for a certain range of solar elevations.
Both relationships, for diffuse and direct radiation, do not change during the growing season.

Table 4. The extinction coefficient for direct radiation K_s in function of the solar elevation (β)

β (°)	0-20	20-30	30-40	40-50	>50
K (-)	0.95	1.05	1.01	0.96	1.05

3.4.5. Submodel LAI-evolution

In this submodel the total LAI value for each of the three considered tree species is calculated during the growing season. The only input parameter is the day number D_n. The seasonal LAI-evolution in function of the day number D_n is given in Fig. 2, and can be described as three linear relationships.
The relative LAI-distribution over the considered canopy layers, remains constant during the growing season for all three species.

3.4.6. Submodel LAI of sunlit and shaded leaves

In this submodel the LAI fractions of sunlit and shaded leaves are calculated for each considered canopy layer. The extinction coefficients for direct PAR and the total LAI for each species are the input parameters.
The leaf area index L_i of canopy layer *i* is then divided in the sunlit $L_{i,sun}$ and shaded $L_{i,shade}$ fraction (m^2 m^{-2}). The LAI of the sunlit leaves, for canopy layer *i*, is calculated as:

$$L_{i,sun} = (e^{-K_s L_{i+1,c}} - e^{-K_s L_{i,c}}) / K_s \qquad (15)$$

The LAI of the shaded leaves, for canopy layer *i*:

$$L_{i,shade} = L_i - L_{i,sun} \qquad (16)$$

where $L_{i,c}$ is the downward cumulative LAI, layer *i* included and K_s is the extinction coefficient for direct PAR.

3.4.7. Submodel PAR interception

In this submodel the PAR intensity intercepted by the leaves is calculated. The inputs to the model are extinction coefficients for diffuse and direct PAR radiation, the hourly incoming PAR intensities (above the canopy), the LAI of sunlit and shade leaves, and the PAR reflection coefficient.

The radiation profile in the canopy can, as mentioned before (see 2.2.2.) be described by the exponential Beer-Bouger Law. For the diffuse PAR radiation, the formula for the calculation of the penetrated intensity can be written as (Goudriaan, 1982):

$$I_{i,d} = (1-\rho_{cd}) I_{o,d} \exp(-K_d . L_{i,c}) \qquad (17)$$

with $I_{o,d}$ the diffuse PAR intensity above the canopy, and $I_{i,d}$ the diffuse PAR intensity at level *i*, $L_{i,c}$ is the downward cumulative LAI at level $_i$, K_d is the diffuese extinction coefficient, and ρ_{cd} (-) the reflection coefficient of the canopy for diffuse PAR.
If the canopy reflection coefficient of total PAR ρ_c is known, ρ_{cd} is calculated as:

$$\rho_{cd} = \rho_c . \frac{0.036}{0.092} \qquad (18)$$

If ρ_c is not known, ρ_{cd} is set equal to the value proposed by de Pury & Farquhar (1997), namely 0.036. The mean ρ_c measured above the mixed deciduous forest Aelmoeseneie during a complete growing season (May - September) amounts to 9.2%.

Every canopy layer is, as mentioned before, divided in two parts: (i) shaded leaves which intercept diffuse light only, and (ii) sunlit leaves which intercept both the diffuse and direct flux (Spitters 1986; Forseth and Norman 1993; Johnson et al 1995; Wang 1996). Intercepted diffuse PAR on level *i* is represented by $I_{i,d}(c)$; for the intercepted direct PAR this is $I_{i,s}(c)$. Both are expressed in µmol m^{-2} s^{-1}. The above can be formulated as:

$$I_{i,sun}(c) = I_{i,d}(c) + I_{i,s}(c) \qquad (19)$$

$$I_{i,shade}(c) = I_{i,d}(c) \qquad (20)$$

with $I_{i,sun}(c)$ the intercepted PAR in sunlit leaves on level *i*, and $I_{i,shade}(c)$ the intercepted PAR in the shaded leaves on level *i*, both are expressed in µmol m^{-2} s^{-1}.

The intercepted direct PAR on level *i* is calculated by multiplying the incoming direct PAR intensity $I_{0,s}$ with the appropriate extinction coefficient (Spitters 1986; Johnson et al. 1995):

$$I_{i,s}(c) = I_{0,s} . K_s \qquad (21)$$

The intercepted diffuse PAR on level *i* can be calculated in several ways. The simplest way, used here, is the approach according to Spitters (1986) and Johnson et al. (1995), where the penetrated diffuse PAR intensity on level *i* ($I_{i,d}$) is multiplied with the extinction coefficient K_d:

$$I_{i,d}(c) = I''_{i,d}.K_d = (1-\rho_{cd})I_{0,d}.e^{-K_d.L''_{i,c}}.K_d \qquad (22)$$

with $I_{0,d}$ (µmol m² s^{-1}) the diffuse radiation above the canopy, ρ_{cd} the reflection coefficient, and $L''_{i,c}$ (m^2 m^{-2}) the downward cumulative LAI in the middle of layer *i*. The penetrated diffuse PAR intensity is calculated using Eq. 17. Using Eq. 22 the mean intercepted diffuse radiation of canopy layer *i* is calculated.

3.4.8. Submodel temperaure dependence of photosynthesis

The temperature dependence of the photsynthesis process is calculated in this submodel. The input is the air canopy temperature. As an output two temperature functions are obtained: one for the gross maximal photosynthesis rate, and one for the respiration rate. The method used by Wang (1996) for the calculation of the photosynthesis of *Pinus sylvestris* is used here.

Temperature function for P_{max}

The temperature dependence of the gross photosynthesis rate is described by Wang (1996):

$$F_{P\max}(T) = \frac{e^{\left(C_1 - \frac{\Delta H_{a,P}}{R_g T}\right)}}{1 + e^{\left(\frac{\Delta S.T - \Delta H_{d,P}}{R_g T}\right)}} \qquad (23)$$

with $F_{Pmax}(T)$:temperature factor for P_{max} (dimensionless [0-1]);
C_1 :constant;
$\Delta H_{a,P}$:activation energy (valid for P_{max}) (J mol^{-1});
R_g : gas constant (J K^{-1} mol^{-1});
T :air temperature (K);
ΔS :entropy of the denaturation equilibrium of CO_2 (J K^{-1} mol^{-1}); and
$\Delta H_{d,P}$ deactivation energy (valid for P_{max}) (J mol^{-1}).

This function has an optimum (F_{Pmax}=1) for a certain temperature. Most parameters in Eq. 23 are species specific, and are adapted here for beech and oak according to the method used by Hollinger (1992). For ash this adaption was not possible because not enough measurements were available. For this reason the parameterisation of Eq. 23 is the same for ash as for oak, as both species prefer light environments. For beech only one temperature function was used. ΔS was choosen so that the sum of the differences between measured and calculated values for the three considered canopy layers of P_{max} equals zero.

An overview of the parameters is found in Table 5. The values of $\Delta H_{a,P}$ and $\Delta H_{a,R}$ are copied from Wang (1996).

Temperature function for R_d

The respiration rate *Rd* (µmol CO_2 m^{-2} s^{-1}) is strongly dependent of temperature. A relationship is given by Wang et al. (1995):

$$F_R(T) = e^{\left(C_2 - \frac{\Delta H_{a,R}}{R_g T}\right)} \qquad \text{(during daytime)} \qquad (24)$$

$$F_R(T) = 1.45 e^{\left(C_2 - \frac{\Delta H_{a,R}}{R_g T}\right)} \qquad \text{(during dark period)} \qquad (25)$$

with $F_R(T)$ temperature function for R_d (dimensionless [0-1]), C_2 is a constant, and $\Delta H_{a,R}$ activation energy (J mol^{-1}). The temperature-dependence of R_d during the nighttime was assumed to have the same response pattern with the respiration rate in light. However a correction coefficient (1.45) was used Wang et al. (1995).

Table 5. The values of the parameters used in the calculations, for the different tree species

Parameters	Beech	Oak and ash
C_1	21.92	21.62
C_2	13.54	13.54
$T_{opt}(P_{max})$ (K)	293.0	298.0
ΔS (J mol^{-1} K^{-1})	709.95	700.00
$\Delta H_{a,P}$ (J mol^{-1})	52750	52750
$\Delta H_{a,R}$ (J mol^{-1})	33870	33870
$\Delta H_{d,P}$ (J mol^{-1})	211000	211000
R_g (J mol^{-1} K^{-1})	8.31	8.31

3.4.9. Annual variation in photosynthesis parameters

α and P_{max} are beleived to change during the growing season:

$$\alpha_i = \alpha_{i,\max}.f(D_n) \qquad (26)$$

$$P_{i,\max} = P_{i,\max,\max}.f(D_n) \qquad (27)$$

where $\alpha_{i,max}$ and $P_{i,max,max}$ are the maximum values of α_i and $P_{i,max}$ respectively during growth season and $f(D_n)$ is a function introducing the annual variation in α_i and $P_{i,max}$. The $f(D_n)$ is expressed as (Wang 1996):

$$f(D_n) = \left(\frac{365 - D_n}{365 - b_1}\right)^{b_2} e^{\left((b_2/b_3)\left[1-(365-D_n/365-b_1)^{b_3}\right]\right)} \qquad (28)$$

where b_1, b_2 and b_3 are parameters, with respective values of 212, 28.4 and 0.21356. The parameters are chosen as such that: (i) maximum values are reached on day 212, (ii) at the beginning of the growing season (day 121) the parameters are already at 50% of their maximum values, (iii) at day 288 the values are at 25% of the maximum values, and (iv) at day 336 (LAI=0) $f(D_n) \leq 0.1\%$.

3.4.10. Leaf photosynthesis

In this submodel the hourly net photosynthesis rate of the sunlit and shaded leaves is calculated for each canopy layer. Input parameters are the hourly intercepted radiation intensities, the functional parameters of the light response curves (at reference temperature), and the hourly temperature functions for P_{max} and R_d. Describing the light response curve using an exponential equation (Goudriaan 1982) gave the best results:

$$P_{n,i,sun} = P_{i,\max}\left(1 - e^{\left(\frac{-\alpha_i . I_{i,sun}}{P_{i,\max}}\right)}\right) - R_i \qquad (29)$$

$$P_{n,i,shade} = P_{i,\max}\left(1 - e^{\left(\frac{-\alpha_i . I_{i,shade}}{P_{i,\max}}\right)}\right) - R_i \qquad (30)$$

with $P_{n,i,sun}$ and $P_{n,i,shade}$ the net photosynthesis rate for sunlit and shaded leaves respectively (µmol CO_2 m^{-2} s^{-1}), $P_{i,max}$ the maximal gross photosynthesis (µmol CO_2 m^{-2} s^{-1}), α_i the initial light efficiency (µmol μmol^{-1}), R_i the respiration rate (µmol CO_2 m^{-2} s^{-1}) and $I_{i,sun}$ and I_i,*shade* the intercepted PAR-intensity for respectively sunlit and shaded leaves (µmol m^{-2} s^{-1}).

As the photosynthesis process is temperature dependent, the photosyntesis rate is calculated as:

$$P_{i,\max}(T) = F_{P\max}(T).P_{i,\max}(Tref) \qquad (31)$$

$$R_i(T) = F_R(T).R_i(Tref) \qquad (32)$$

with $P_{i,max}(T)$ and $R_i(T)$ respectively the values of $P_{i,max}$ and R_i at air temperature T and $P_{i,max}(Tref)$ and $R_i(Tref)$ values for respectively $P_{i,max}$ and R_i at their reference temperatures. For $P_{i,max}$ the reference temperature is 20°C for beech and 25°C for oak and ash (Table 5). In the case of R_i the reference air temperature is 20°C for all species.

3.4.11. Canopy photosynthesis

The total net photosynthesis is calculated by addition of the photosynthesis on leaf level for the different canopy layers. Cumulative values are obtained by integration of all hourly values during the considered time period.

Input factors are the net photosynthesis rate for sunlit and shaded leaves for the considered canopy layers, as well as the corresponding LAI values for the considered leaves and canopy layers. The output is the hourly net canopy photosynthesis rate $P_c(t)$ (µmol CO_2 m^{-2} s^{-1}) and the cumulative net uptake of CO_2 $P_{c,cum}$ (µmol CO_2 m^{-2} s^{-1}):

$$P_c(t) = \sum_{l=1}^{3}\left[\left(P_{n,i,sun}.L_{i,sun}\right) + \left(P_{n,i,shade}.L_{i,shade}\right)\right] \qquad (33)$$

$$P_{c,cum} = \int_0^t P_c(t)dt \qquad (34)$$

Using the relative occurrence of the three considered species in the forest, the net CO_2-uptake of the forest can be calculated, assuming that the forest only consist of these tree species.

4. Discussion

Measurements of the SLA of beech leaves (Table 1) reveal that leaves at the top of the canopy are clearly morphologically different from leaves found deeper in the canopy. The same difference, but somewhat lower values were found by Harley & Baldocchi (1995) for leaves of white oak (*Quercus alba* L.). Hutchison et al. (1986) even found a lower SLA value (0.008 $m^2 g^{-1}$) also for leaves of white oak at the top of canopy. The SLA of beech used as input to the FORGRO model is 0.0170 $m^2 g^{-1}$ (Bartelink et al. 1997). The SLA of ash and oak was not examined because their canopies were only accessible from Level 3. Nevertheless a difference is expected, as the difference found by Harley & Baldocchi (1995) were from leaves at the top of the canopy and 3-4 m down. It is important to note that the terms sun-adapted (shade-adapted) and sunlit (shaded) leaves are not identical. The former term refers to the morphology (and related physiology) of the leaves, where the latter term refers to the illumination of the leaves.

The initial quantum efficiency (Table 2) increases with depth in canopy (measurements at 20°C). A higher quantum efficiency is typical for shade-adapted leaves which are found deeper in the canopy. The values found at Layer 3 corresponds well with the mean quantum efficiency for C_3 leaves, namely 0.073 (Ehleringer & Björkman 1977), but are higher than the values found by Harley & Baldocchi (1995). The maximal gross photosynthesis rate for oak is very similar (11.5 μmol $m^{-2} s^{-1}$) to the values found by Harley & Baldocchi (1995) for the sun adapted leaves of white oak. For the shade-adapted leaves a significant lower value was found (7.9 μmol $m^{-2} s^{-1}$). This decrease with depth in the canopy was clearly observed for beech. Harley & Baldocchi (1995) found the temperature optimum for the net photosynthesis rate of white oak to be 25°C, which corresponds with our findings for oak. According to the same authors, when expressed per unit dry weight, the photosynthesis rates observed at the different canopy depths should be equal. In our findings the rates at Layer 1 and 2 are almost equal, but clearly higher than the rate measured at Layer 3. In general the rate of dark respiration should be lower in shade-adapted leaves, reflecting reduced physiological activity (Boardman 1977). This agrees with our measurements, although no significant difference is found.

Little information is available about the distribution of LAI in function of depth in the canopy. This is due to the relative inaccessibility of the canopy crowns combined with the labour intensity of the work.Table 3 indicate that the majority of the LAI is found in the top of the canopy. This is consistent with results of Hutchison et al. (1986). Many values for the maximal LAI are found in literature, but they can vary a lot, even for identical forest types. Dufrêne & Bréda (1995) found for an old mixed forest of *Quercus petraea* and *Fagus sylvatica* an LAI of 5.86. for mixed deciduous forests mainly consisting of *Quercus* sp.values of 3.5, 3.58 and 4.89 were respectively found by Hutchison et al. (1986), Wang et al. (1992) and Chason et al. (1991). The proposed seasonal LAI-evolution, illustrated in Fig.1, is comparable with the one used by Ogink-Hendriks (1995) for an oak forest in The Netherlands. This author found for two growing seasons a maximal LAI of 4.9. The choice of May 1 as the starting date for leaf development is realistic, surely for beech (Kramer 1994).

The extinction coefficients for diffuse PAR (Table 4) reveal no dependence of solar elevation. The mean K_d corresponds very well with the value found by Baldocchi et al. (1984), namely 0.73, and with the value used as input to the FORGO-model (0.65)(Bartelink et al. 1997). For the direct PAR, a complex dependence of the solar elevation is found. The observed trend do not correspond with what can be expected from mathematical models (e.g. a spherical leaf angle distribution). According to Baldocchi et al. (1984) deviations from theory can be attributed to clumping and gaps in the canopy.

The size and shape of canopy elements and the manner in which they are displayed in space and time, along with their optical characteristics, are of great importance to ecosystem structure and function. These characteristics affect canopy-atmosphere exchanges of electromagnetic radiation (Hutchison et al. 1986). If a model was used to calculte the extinction coefficients, clumping and the vertical change in e.g. leaf area distribution should be known, which is not evident. If these characteristics are not taken into account, errors are likely to occur, causing the radiation profile in the canopy to be described incorrectly, and thus also the canopy photosyntheis. To avoid the above mentioned problems, and because these architecture characteristics are complex in a deciduous mixed forest stand, it was preferred to measure the extinction coefficients, rather than to model them. Measurements integrate the complete architecture. Spitters (1986) also preffered a measured value for K_d above a theoretical one.

As the model is only used in the growing season (foliated period), the extinction coefficients are thought to remain constant during this period.
The used temperature functions (Eqs 23, 24 & 25). , and the function describing the annual variation in the photosynthesis parameters (Eq. 28), should be further tested to refine the parametrisation. For the temperature functions this could be done by measurements of photosynthesis rate at different temperatures. The second function can be refined by repeated photosynthesis measurements (under controlled environment) during the growing season.

Just as in the FORGRO model the photosysnthetic rate is derived from the photosynthesis-light response curve, described by a negative exponential function (Bartelink et al. 1997). Contrary to the MAESTRO model of Wang & Jarvis (1990), the FORUG model considers no horizontal heterogenity. Introduction of horzontal heterogenity requires a consideralbe increase of the input data. An increase of input data is coupled with an increase of the model uncertainty if, as is the case here, these data can not be determined appropriately.
The FORUG model described in this paper will be validated against *in situ* measurements of leaf photosynthesis in a companion paper (Samson et al. 1997). In this paper also simulation results will be discussed.

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Appendix A. Abbreviation units and definitions of symbols

Term	Units (Values)	Definition
d		Distance to the sun at any times
d		Yearly averaged distance between the sun and the earth
D	-	Diffuse fraction of Rs
D_n	d	Day number since beginning of year
E_t	min	Equation of time
h	degrees	Hour angle of the sun
h_s	degrees	Hour angle of the sun at sunset
I_d	µmol m^{-2} s^{-1}	Diffuse PAR per unit ground area
I_o	µmol m^{-2} s^{-1}	Total PAR above the canopy per unit ground area
I_s	µmol m^{-2} s^{-1}	Direct PAR per unit ground area
$I_{(c)}$	µmol m^{-2} s^{-1}	Intercepted PAR per unit leaf area
$I_{shade(c)}$	µmol m^{-2} s^{-1}	Intercepted PAR by shaded leaves per unit leaf area
$I_{sun(c)}$	µmol m^{-2} s^{-1}	Intercepted PAR by sunlit leaves per unit leaf area
K_d	-	Diffuse PAR extinction coefficient of canopy
K_s	-	Direct PAR extinction coefficient of canopy
L	m^2 m^{-2}	Leaf-area index
L_e	degrees (3°49'30")	Standard longitude of time zone
L_{shade}	m^2 m^{-2}	Leaf-area index of shaded leaves
L_s	degrees (winter period: 15 ;summer period: 30)	Local longitude (Gontrode, Belgium)
	m^2 m^{-2}	
L_{sun}	µmol m^{-2} s^{-1}	Leaf-area index of sunlit leaves
P_c	µmol m^{-2} s^{-1}	Rate of net canopy photosynthesis per unit ground area
P_{max}	µmol m^{-2} s^{-1}	Rate of maximal gross leaf photosynthesis per unit leaf area
P_n		Rate of net leaf photosynthesis per unit leaf area
	µmol m^{-2} s^{-1}	Rate of leaf respiration per unit leaf area
R	J m^{-2} s^{-1}	Extra-terrestrial solar radiation intensity
R_a	MJ m^{-2} d^{-1}	Extra-terrestrial solar radiation on a daily basis
$R_{a,d}$		Gas constant
	J mol^{-1} K^{-1} (8.314)	Shortwave radiation intensity
R_g	J m^{-2} s^{-1}	Shortwave radiation day sum
R_s	MJ m^{-2} d^{-1}	Solar constant
$R_{s,d}$	J m^{-2} s^{-1} (1370)	
SC	MJ m^{-2} d^{-1} (118.1)	Time of day
	h	Time of solar noon
t	h	Air temperature

t_o	K	Initial light efficiency
T	μmol μmol^{-1}	Solar elevation angle
α	degrees	Solar declination
β	degrees	Activation energy
δ	J mol^{-1}	Deactivation energy
ΔH_a	J mol^{-1}	Entropy of the denaturation equilibrium of CO_2
ΔH_d	J mol^{-1} K^{-1}	Latitude (Gontrode, Belgium)
ΔS		Canopy reflection coefficient for total PAR
	degrees (50°58'35")	Canopy reflection coefficient for diffuse PAR
λ	-	
ρ_c	-	
ρ_{cd}		

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