Scaling leaf photosynthesis to canopy in a mixed deciduous forest.
II. A simulation study for two growing seasons

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Abstract

The model as described in Samson et al. (1997) (FORUG model) is validated at the leaf level, and seems to simulate well the canopy rates for the different species and the different considered layers in the canopy. The highest instantaneous canopy photosynthesis rates are found for oak, the lowest for beech. The total amount of carbon assimilated during the growing season was highest for oak and ash and lower for beech and amounted respectively 10.9, 11.0 and 10.3 ton C ha^{-1} y^{-1} for the growing season 1996. The carbon uptake was higher during the growing season 1997 due to a higher mean daily temperature, and a higher amount of incoming PAR. For bole respiration the maximum rate for both growing seasons amounted 3.6 µmol m^{-2} s^{-1}. Integrated over the growing season the total bole respiration amounted 4.5 and 4.3 ton C ha^{-1} y^{-1} for respectively the growing season 1997 and 1996.
At high temperatures and high PPFD, temperature becomes a limiting factor for Net Canopy Photosynthesis (NCP). A total forest canopy has, just as leaves, a curvilinear reaction on PPFD. This finding allowed to construct a one-layer or 'big leaf' model which simulated the NCP as well as did the multi-layer FORUG model. However a multi-layer model for simulating the NCP is preffered as it allows more simpler incorporation or adaptation of parameters.

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

1. Introduction

Estimation of the net CO$_2$ exchange rates of the canopy over longer periods is important in gaining a better understanding of how the vegetation will respond to changed environmental conditions and in improving the ability to predict biomass production under changing climate conditions in the future (Wang 1996). Simulation models, scaling up leaf level information to the canopy, have a great potential for estimation of these CO$_2$ exchange rates.
When the models are used to predict long-term responses of canopies to environmental perturbations such as increased global CO$_2$ concentrations and temperature, the reliability of the prediction is largely related to plant materials used in the model parameterization. But either if leaf level information is correct, a definitive test to leaf-to-canopy integration and scaling schemes is lacking (Baldocchi & Harley 1995); either micrometeorological flux measurements have been unavailable to test the integration and scaling schemes (Hollinger 1992) or insufficient *in situ*

measurements of leaf physiological processes were obtained to parametrize model calculations (Baldocchi 1993).

Physiological and optical parameters are frequently known at the scale of individual leaves, shoots or plants, but not at the vegetation scale, because they are determined from measurements made in a cuvette or chamber (Kruijt et al. 1997). In general, parameters at canopy scale are not identical to parameters at leaf scale, and they cannot be treated as simple averages or totals of the parameters of all leaves in the canopy. This is due to the fact that leaves in a canopy are not independent but interact with each other, and secondly several processes that are defined by leaf scale parameters respond non-linearly to environmental variables within a canopy (Kruijt et al. 1997). A useful approach, therefore, is to develop a 'big leaf' model using leaf-scale parameters through 'bottom-up' scaling (Berry et al. 1997).

The objectives of this paper are: (i) to validate the multi-layer and bottom-up FORUG model as described in Samson et al. (1997), (ii) to use this model to quantify the net CO_2 uptake by the photosynthesis proces for three different deciduous tree species, namely beech (*Fagus sylvatica* L.), oak (*Quercus robur* L.) and ash (*Fraxinus excelsior* L.) and for a mixed deciduous forest ecosystem for two growing seasons (1996 and 1997). A third (iii) objective is to check whether from the data obtained by the model simulations a big-leaf model, and its parameters, can be deducted.

2. Materials 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 an 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-beech and the ash forest type during the 1996 growing season was 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. Meteorological measurements

The meteorological data used as input to the model as described in Samson et al. (1997) are the hourly averages of shortwave radiation, and the corresponding albedo coefficients, and mean hourly air temperature on top of the canopy.

The shortwave radiation (incoming and reflected) is measured each minute ± 10 m above the canopy with an albedometer (GS2, Delta-T). The air temperature in the canopy is measured every minute and averaged over a half hourly period. Temperature measurements were executed at Layer 3 with a shielded Pt100 sensor.

2.3. Gas exchange measurements

For validation of the leaf gas-exchange model, the rate of photosynthesis is also measured *in situ* on different levels of the canopy. Only fully expanded leaves were sampled. The measurements were executed during the summer of 1997, using a commercially available gas-exchange system (WALZ,G). This system consisted of a fan-stirred cuvette (PMK-10, WALZ) attached to a measurement and control system (CQP-130, WALZ). Water vapour and CO_2 exchanged by the leaf are measured with an IRGA (BINOS-100/4P, WALZ), also in the differential mode.The outside microclimatological conditions were tracked in the cuvette.

2.4. Bole respiration

Beside canopy photosynthesis and soil respiration, bole respiration is an important process in the exchange of CO_2 between the forest and the atmosphere. Baldocchi & Harley (1995) computed bole respiration for a mixed deciduous forest near Oak Ridge, TN, USA, using algorithms from Edwards & Hanson (1995) and biomass information from Johnson & Henderson (1989). Baldocchi & Harley (1995) assumed the reference bole respiration rate at 10 °C to equal 1.86 μmol m^{-2} s^{-1} (on a ground area basis).

For the calculation of the bole respiration during the growing season, the above reference values were used, combined with a temperature function for R_d during dark period (Wang et al. 1995):

$$F_R(T) = 1.45e^{\left(C_2 - \frac{\Delta H_{a,R}}{R_g T}\right)}$$

with $F_R(T)$ temperature function for R_d (dimensionless [0-1]), C_2 is a constant (14.651), $\Delta H_{a,R}$ activation energy (33870)(J mol^{-1}), T air temperature (K) and R_g the gas constant (8.31)(J K^{-1} mol^{-1}).

Bole respiration was calculated using daily mean temperatures measured at the ground level of the forest (shielded Pt100).

3. Results

3.1. Model validation at the leaf level

Each model has to be tested, to have an idea about the exactness of the output data. For this purpose leaf gas exchange was measured *in situ* on different levels in the canopy during the 1997 growing season. The meteorological conditions measured during the field campaign, are used as input to the leaf photosynthesis submodel of the FORUG model. In contrary to the hourly averages used as input data to the model, meteorological conditions in the canopy are changing very quickly (Fig. 1).

The agreement between the measured and modelled leaf photosynthesis rate is illustrated in Figure 2 and Figure 3 for beech and oak respectively. From Figure 2 it can be seen that the correspondance between the measured and modelled values is quite good.

On Layer 3 the correspondance is somewhat less than for the other two layers. On Layer 3, at lower PPFD (Photosynthetic Photon Flux Densities) values the leaf photosynthetic rate is overestimated by the model while at higher PPFD levels, the reversed is observed.

At Layer 2 more or less the same tendency is observed, althought the relation is closer to 1:1. At intermediate photosynthesis rates more scattering is observed.

At the lowest canopy layer, Layer 1, both methods agree very well, only at higher photosynthesis rates there is a tendency for underestimation by the model, while again more scattering is observed at intermediate photosynthesis rates. The photosynthesis rates for ash are slightly overestimated.

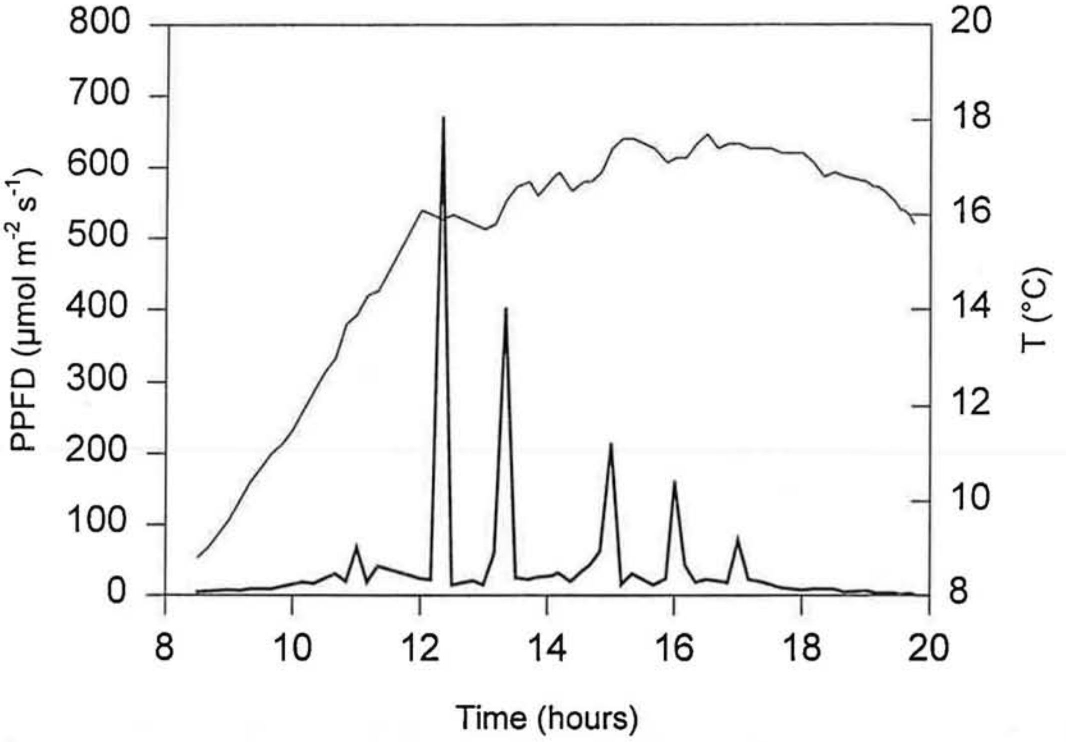

Figure 1. Measured air temperature and PPFD in the canopy (Layer 1), on 9 September 1997

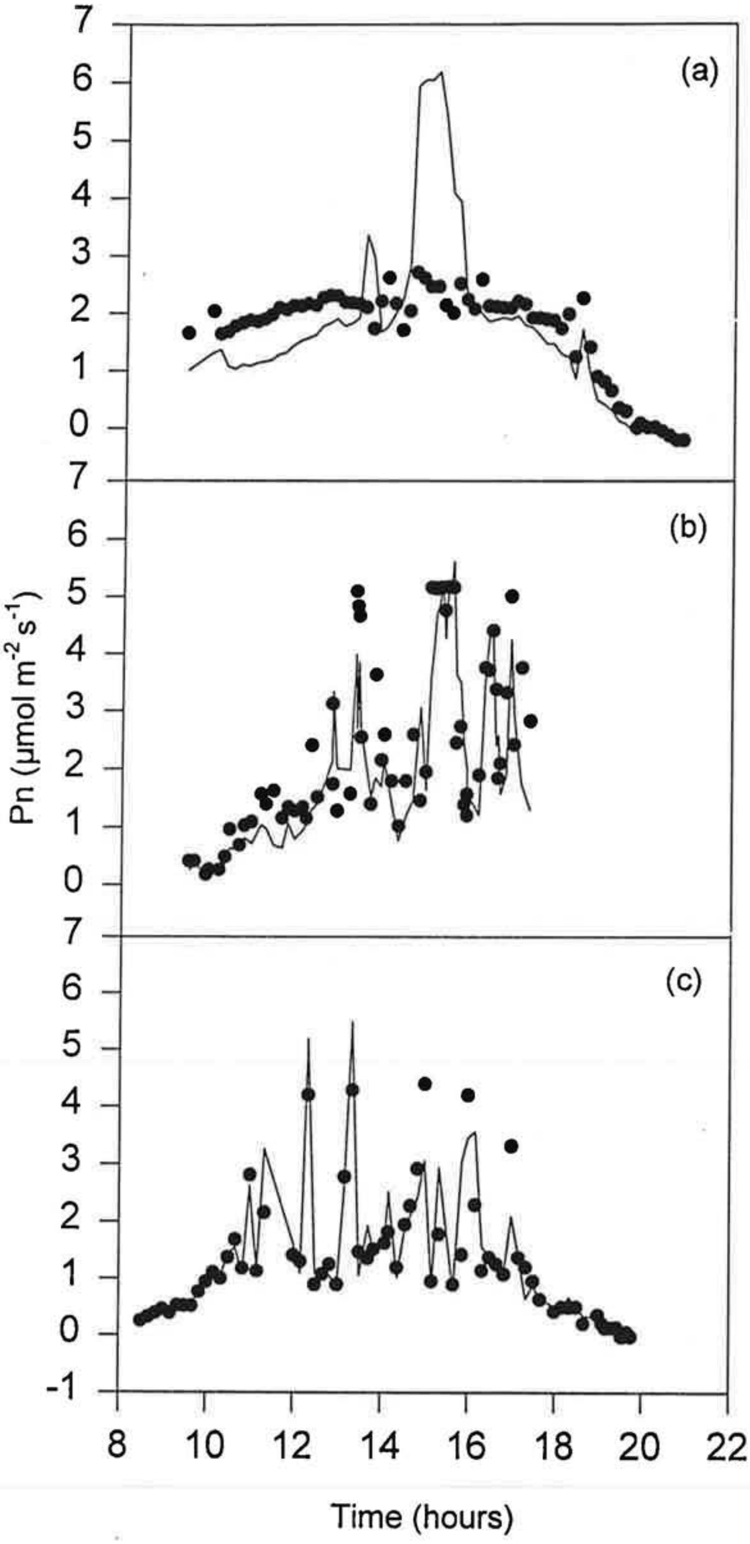

Figure 2. A comparison between field measurements (solid lines) and model simulations (closed circles) of the leaf photosynthesis rate of beech. (a) Measurements on Layer 3 on September 9. (b) Measurements on Layer 2 on September 8. (c) Measurements on Layer 1 on September 10

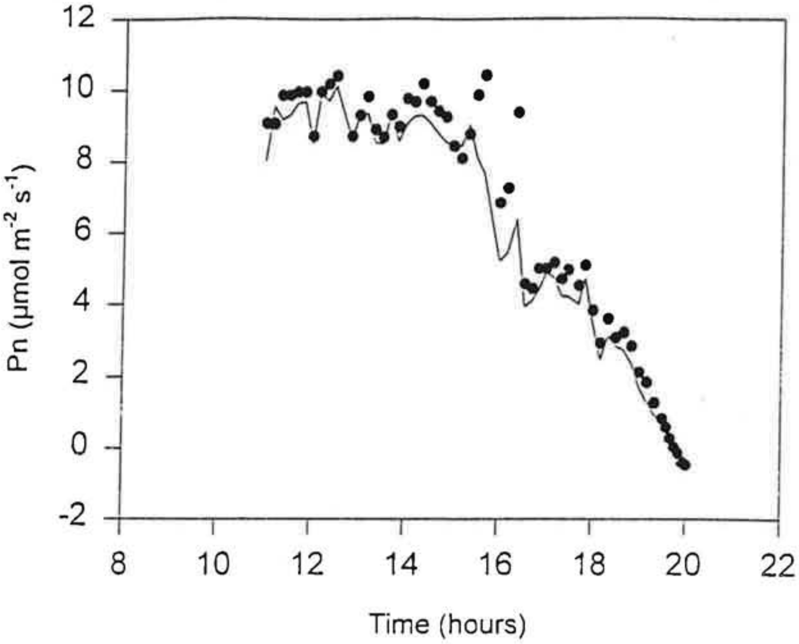

Figure 3. A comparison between field measurements (solid lines) and model simulations (closed circles) of the leaf photosynthesis rate of ash on Layer 3 (September 11)

3.2. Model predictions

The diurnal pattern of net canopy photosynthesis for beech, oak and ash is illustrated for a sunny (July 21 1996) and a cloudy day (August 30 1996) in Figure 4.

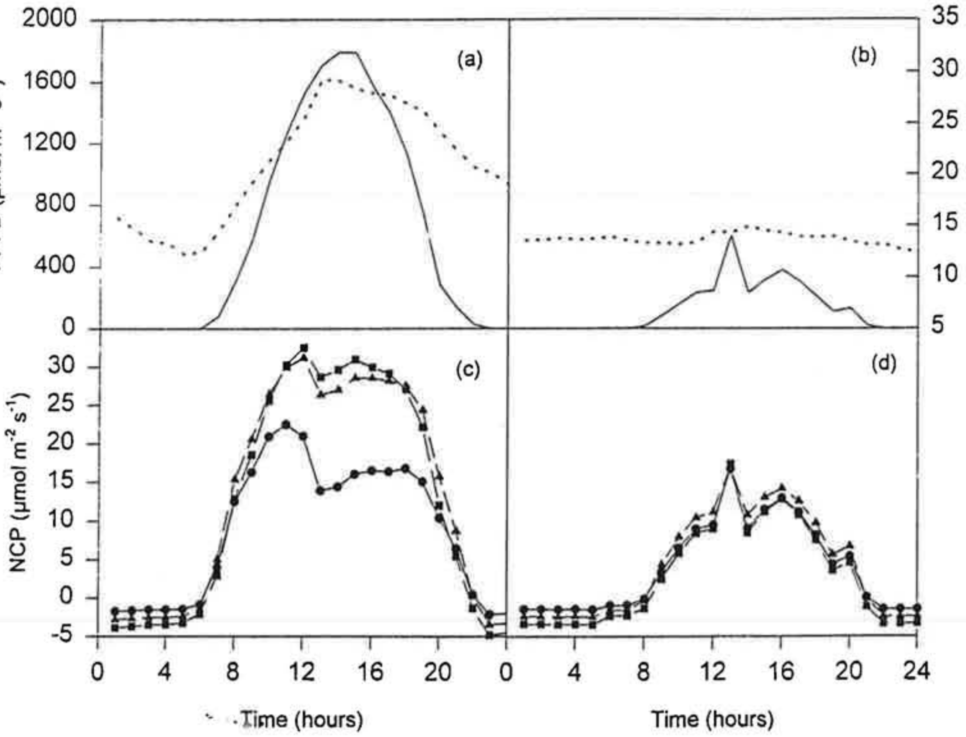

Figure 4. Hourly mean values of PPFD on top of canopy (solid line) and air temperature (Layer 3)(dashed line): (a) measured on a sunny day (June 21 1996), and (b) a cloudy day (August 30 1996). The corresponding hourly mean values of net canopy photosynthesis for beech (closed circles), oak (closed squares) and ash (closed triangles). (c) Simulations for a sunny day (June 21 1996). (d) Simulations for a cloudy day (August 30 1996).

On both days ash has the highest net canopy photosynthesis (NCP) rate in the morning and the late afternoon. On the cloudy day ash has even the highest NCP rate during midday, while on the sunny day oak has the highest midday NCP. During nighttime oak has the highest respiration rates, and beech the lowest. On the sunny day higher NCP rates were obtained for all three species, compared to the cloudy day.

The seasonal dynamic of NCP and bole respiration is illustrated in Figure 5, for both 1996 and 1997. The results shown in Figure 5, are simulations for a theoretical mixed deciduous forest for respectively 19%, 36 % and 45% consisting of beech, oak and ash. These species composition is very similar to the natural composition occurring in the experimental forest. From the figures it is clear that the NCP is a very dynamical process. This can be understood by the fact that NCP is dependent on several factors, e.g. LAI, PPFD, temperature,.... These factors all have a diurnal and/or seasonal behaviour. Bole respiration also shows a dymical behaviour during the growing season as it is mainly (and in this simulation model-only) dependent on temperature. During most part of the growing season NCP exceeds bole respiration.

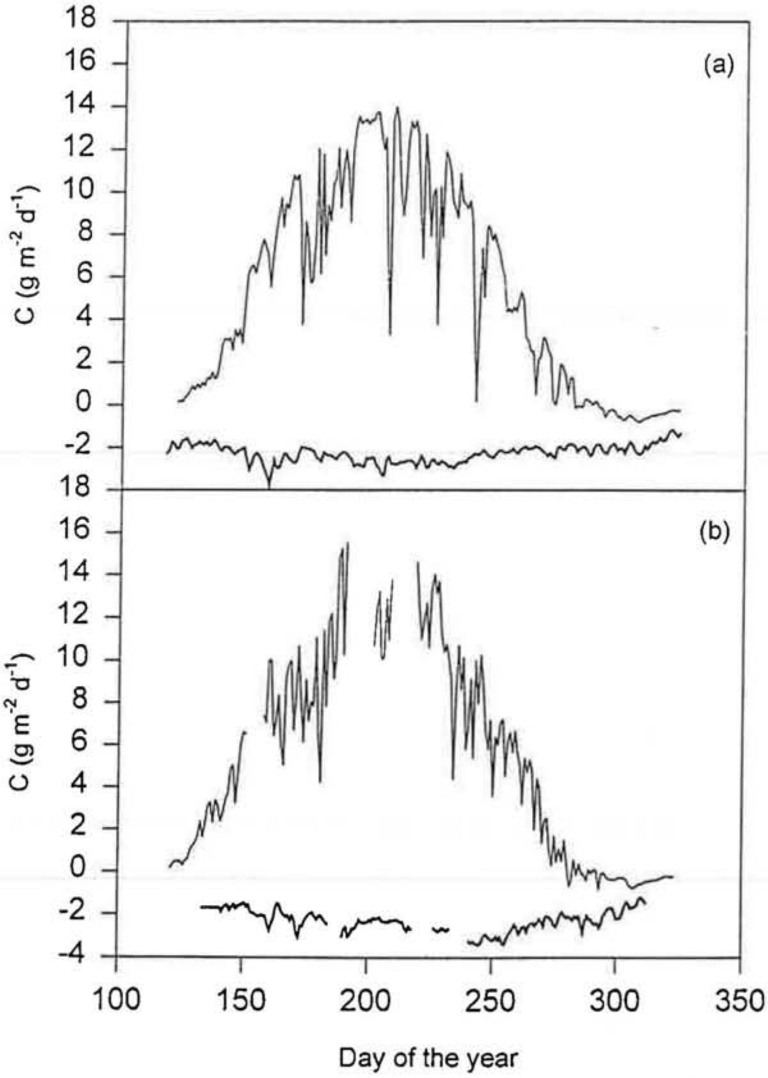

Figure 5. Simulation results for a theoretical mixed deciduous forest (19% beech, 36% oak and 45% ash). (a) Seasonal pattern of NCP (thin line) and bole respiration (thick line) for the growing season 1996. (b) Seasonal pattern of NCP and bole respiration for the growing season 1997.

The simulated maximum rates of NCP amounted for beech, oak and ash respectively 30.3, 42.8 and 35.7 µmol m^{-2} s^{-1}. For bole respiration the maximum rate for both growing seasons amounted 3.6 µmol m^{-2} s^{-1}. Maximum hourly rates of bole respiration can be somewhat higher, but will probably not exceed 6 µmol m^{-2} s^{-1}. The total amount of carbon assimilated during the growing seasons 1996 and 1997 is given in Table 1, for each species, an oak-beech forest type (66% oak, 34% beech) and a theoretical mixed deciduous forest (19% beech, 36% oak and 45% ash). In both years beech has the lowest NCP, while the values for oak and ash are very similar. For all species, the NCP in 1997 is considerably higher then in 1996. Also bole respiration is highest during the 1997 growing season (May 1- October 31), namely 4.5 ton C ha^{-1} y^{-1}, compared to 4.3 ton C ha^{-1} y^{-1} during the growing season 1996.

Table 1. Total amount of carbon assimilated (ton C ha^{-1} y^{-1}) during the growing season 1996 and 1997 for beech, oak , ash, a theoretical oak-beech forest (66% oak, 34% beech), and a theoretical mixed deciduous forest (19% beech, 36% oak, 45% ash)

Growing season	Beech	Oak	Ash	Oak-Beech	Mixed forest
1996	10.3	10.9	11.0	10.7	10.8
1997	11.0	12.2	12.1	11.8	11.9

3.3. Environmental control of NCP

In Figure 6 the dependence of NCP on air temperature is illustrated for a beech forest and a theoretical mixed deciduous forest (defined above), for a ten day period (July 15-24 1996). Above 20 °C, temperature becomes the limiting factor for canopy photosynthesis of beech. For a mixed deciduous forest the temperature optimum becomes broader, due to the mixing of several species, each with its own characteristic temperature optimum.

The dependence of NCP on PPFD (Figure 7) is clear, with an increasing NCP as PPFD increases. At higher PPFD values more scattering is observed. This can be explained by the fact that higher PPFD values are mostly corresponding with high air temperatures, causing NCP to be depressed by increased respiration.

Calculated NCP was a curvilinear function of incoming PPFD (Figure 7). The function has the shape of a typical light response curve. The NCP light response curve can described by an exponential equation (Goudriaan 1982), just as for the response of photosynthesis on the level of the indiviual leaf. The obtained canopy photosynthesis parameters, initial quantum efficiency, maximal gross photosynthesis rate and rate of dark respiration amount to respectively 0.078 µmol $µmol^{-1}$, 33.69 µmol m^{-2} s^{-1} and 2.69 µmol m^{-2} s^{-1}. Except for the initial quantum efficiency, the obtained values are considerable higher than the values obtained at the leaf level (Samson et al. 1997).

The exponential equation, as described above, combined with (i) a temperature funtion for the gross maximal photosynthesis rate and (ii) respiration rate, and (iii) a function describing the annual variation in the photosynthesis parameters (see Samson et al. 1997) can be considered as a one-layer model or a 'big leaf' model. The parameters of the temperature functions are determined taking into account the abundance of the different species in the theoretical mixed forest. In Figure 8 a comparison is made between the NCP values obtained using the multi-layer FORUG model and the one-layer model as described above. The figure illustrates that the simulation results are very comparable. This result suggest that a one-layer model is more interesting to use in comparison to a multi-layer model, because of the simularity of the results and the simplicity of the one-layer model.

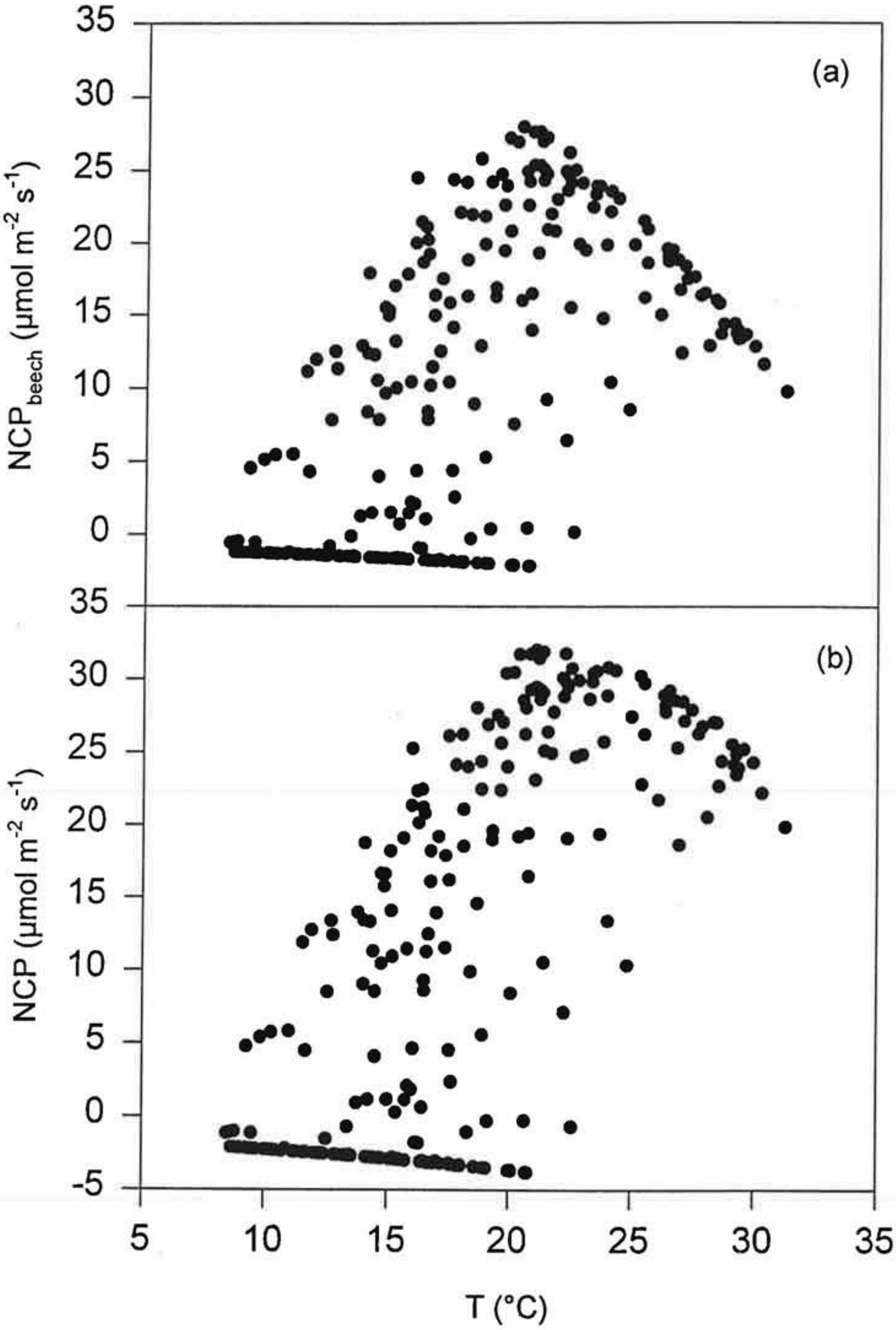

Figure 6. NCP in function of air temperature (Layer 3) for (a) a beech forest and (b) a theoretical mixed deciduous forest (19% beech, 36% oak and 45% ash), for the period (July 15-24 1996)

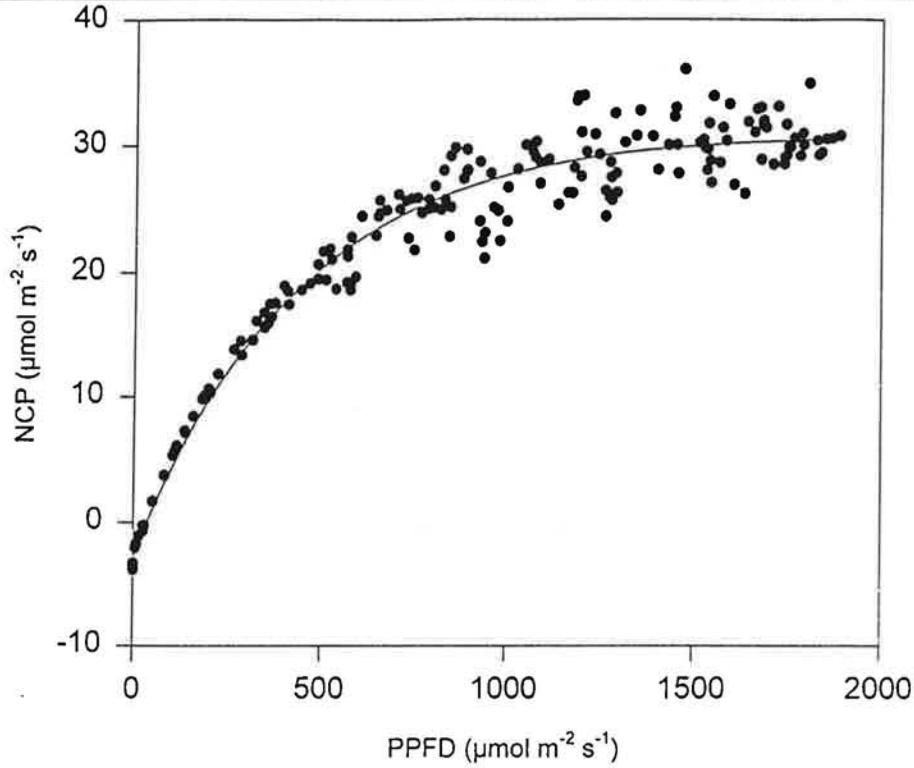

Figure 7. The dependence of NCP on incoming PPFD, within the temperature range 18-27 °C, for a theoretical mixed deciduous forest (19% beech, 36% oak and 45% ash). The solid line is the fitted canopy light response curve, the solid circles are obtained from simulations with the FORUG model for the period July 15 - August 3 1996

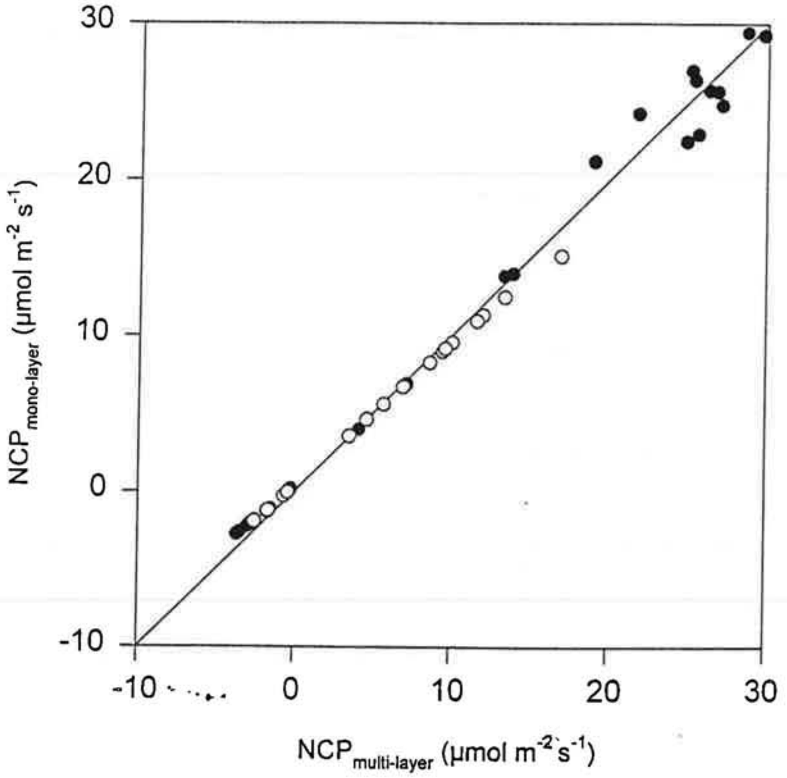

Figure 8. A comparison between simulation results of NCP obtained with the multi-layer FORUG model and a mono-layer model, for a sunny day (closed circles)(June 21 1996), and a cloudy day (open circles)(August 30 1996)

4. Discussion

As the FORUG-model describes the exchange of CO_2 due to photosynthesis between the entire tree or forest canopy and the atmosphere, the model should be validated at the stand scale by e.g. micrometeorological flux measurements. Analysis of the CO_2 exchange between forest and atmosphere is ongoing, but these data also include the exchange of CO_2 due to soil and bole respiration , beside the photosynthetic CO_2 exchange. Therefore the model is only valdidated at the leaf scale. Harley & Baldocchi (1995) also validated their model results with field measurements of gas exchange in a forest canopy (white oak). Figure 2 and Figure 3 illustrates that the model is able to simulate the dynamic behaviour of photosynthesis at the leaf level. Although the complex dependence of photosynthesis to several parameters e.g. temperature, time period in the growing season,...and although the very small sample size compared with the leaf-to-leaf variation in leaf gas exchange, the photosynthesis process is well described by the model. For beech at Layer 3 photosynthesis rates are systematically overestimated by the model, except for higher photosynthesis rates where the opposite is observed. The higher scattering at intermediate leaf photosynthesis rates can be explained by the fact that they occur at intermediate levels of PPFD. Intermediate levels of PPFD are frequently observed in periods of half cloudy, or windy conditions. These conditions cause a very quickly changing pattern of sun and shade flecks. In these conditions the apparatus can registrate e.g. a low PPFD value while the leaf is still having a higher photosynthesis rate from the period before when it was situated in a sunfleck. At lower PPFD values the radiation is mainly diffuse, causing less variability in the behaviour of sun and shade flecks, and thus stabilizing the photosynthesis rate. At higher PPFD intensities the sky is rather cloudiless, having the same result as for low PPFD intensities.

Comparing the NCP results for a sunny and a cloudy day (Fig. 4) reveals that the highest rates are found on the sunny day as could be expected, due to the high values of PPFD. The midday depressions on the sunny day are caused by a higher temperature, driving respiration. While in reality the midday depressions are also due to stomatal closure, which in this regard is an indirect reaction on a higher temperature. The midday depression in NCP is most pronounced for beech as this species has the lowest temperature optimum (20°C) which is clearly exceeded during most of the daytime. Taking into account the daysum of PAR, the photosynthesis process is much more effective for the cloudy day. This effectiviness can be expressed as a Radiation Use Efficiency (RUE), which is here defined as the amount of carbon fixated during a day to the amount of incoming PPFD. For the sunny day the RUE amounts then 0.76, 1.11 and 1.65 g C MJ^{-1} PAR, where the RUE for the cloudy day amounts 1.71, 1.24 and 1.83 g C MJ^{-1} PAR for beech, oak and ash respectively.

Baldocchi (1997) found rates of net ecosystem CO_2 exchange of a broad-leaved forest to exceed 20 $\mu mol\ m^{-2}\ s^{-1}$ around midday in spring, when soil moisture was ample. This value corresponds well with our findings, taking into account net canopy photosynthesis, bole respiration and soil respiration.

The dynamic behaviour of the canopy photosynthesis (Fig. 5) found with the FORUG model corresponds well with simulation results obtained with the FORGRO model for beech (Bartelink et al. 1997), and with the results of Wang (1996) for Scots pine. A major difference between the FORUG and the FORGRO model seems to be the simulation of LAI in the beginning and at the end of the growing season. The more gradually increase and decrease of the LAI used in the FORUG model seems to be more realistic, and corresponds well with observations in the field. The carbon fixation by the canopy simulated with the FORUG model corresponds with eddy correlation measurements above a deciduous forest (Wofsy et al. 1993). These authors found a gross ecosystem production of 11.1 ton C ha^{-1} y^{-1}.

The higher carbon fixation observed during the growing season 1997 compared to the growing season 1996 (Table 1) can be explained by the higher total amount of incoming radiation and the higher mean temperature during this growing season. The higher mean temperature also explains the higher bole respiration rates observed during the growing season 1997. It should be remarked that for the calculation of bole respiration the used reference value as well as the temperature function and its parameters are taken from literature. Results therefore only give an indication about the dynamic behaviour of bole respiration and the order of magnitude of the results. The more theoretical approach used here should be checked with field measurements.

In Fig. 6 the widespread ecological principle is illustrated, stating that an ecosystem consisting of several species is more stable than a monspecies community. In a multi-species forest ecosystem C-uptake from the atmsophere will be more buffered to changes in temperature. Baldocchi (1997) also found that rates of net ecosystem exchange were optimal when air temperature ranged between 22 and 25°C.

A comparable response between PPFD and canopy photosynthesis, as illustrated in Fig. 7, is found by Baldocchi & Harley (1995). The maximal photosynthesis rate, as can be found from their Fig. 12, reaches ± 30 µmol m^{-2} s^{-1}, which is very close to our value of gross maximal photosynthesis, namely 33.69 µmol m^{-2} s^{-1}. On the leaf level as well as on the canopy level, net photosynthesis was a curvilinear function of incomming PPFD. This was also reported by Baldocchi & Harley (1995). This response differs from observations made over crops, which show a highly linear response to PPFD (Denmead 1976, Baldocchi 1994). The curvilinear response of photosynthesis of forest canopies to PPFD, can be explained by the fact that the canopies exists of sunlit and shade leaves. Sunlit leaves, by definition, receive direct radiation regardless of depth in canopy, causing saturation of leaf photosynthesis over a broad range of irradiance. As shaded leaves mostly intercept low irradiance levels, they are not light saturated, causing photosynthesis to react linearly to PPFD. An increase of incomming PPFD, may saturate photosynthesis of shaded leaves at top of the canopy, but deeper in the canopy there will still be shaded leaves which are not light saturated. Thus, the integrated photosynthesis responses of all shaded leaves in the canopy to PPFD is linearly. Superimpossing the reactions of sunlit and shaded leaves to each other explains the curvilinear reaction of the canopy as described above. The LAI of a forest being higher than one, and the occurrence of sunlit and shade leaves, explains why the simulated photosynthesis rates for a canopy is much higher than the leaf photosynthesis rates.

Apparently the canopy photosynthesis can be as good simulated with a one-layer model as with a multi-layer model (Fig. 8).So, it seems to be very attractive to simulate net canopy photosynthesis making use of this one-layer model, as it considerably simplifies the calculations. However it should be remarked that the one-layer model is only checked, and thus valid, for a limited period, with stable LAI. So the parameters for the one-layer model should be at least calculated for three periods: increasing, stable and decreasing LAI. Multi-layer models allow (easy) adaptation of e.g. stand characteristics as vertical LAI distribution, whereas mono-layer models need to be totally re-parameterized in this case. Moreover, the flexibility of multi-layer models allow within-canopy profiles of both environmental and physiological variables to be incorporated (de Pury & Farquhar 1997). The use of one-layer models can thus be interesting for the forest and the period for which they are constructed, but multi-layer models are preferred as they are less rigid.

5. Acknowledgements

The cooperation of J. De Bie and M. Vanoverbeke during the gas exchange measurements, and the technical support of P. Deman is gratefully appreciated
Research and experimental set-up in the Aelmoeseneie forest are sponsored by the University of Ghent, The Flemmisch Community (Contract No B&G/15/1995), the Federal Office for Scientific, Technical and Cultural Affairs (Contract No GC/DD/05a) and the European Community (Contract No IBW/1/1997).

6. Bibliography

Baldocchi, D.D. (1993). Scaling water and carbon exchange from leaves to canopy: rules and tools. p.77-114. In J. Ehleringer & C.B. Field, eds. Scaling Physiological Processes: Leaf to Globe. Academic Press, London.

Baldocchi, D.D. (1994). A comparative study of mass and energy exchange rates over a closed C_3 (wheat) and and open C_4 (corn) crop. II. CO_2 exchange and water use efficiency. Agricultural and Forest Meteorology, 67, 291-321. Source: Baldocchi, D.D. & Harley, P.C. (1995).

Baldocchi, D.D. (1997). Measuring and modelling carbon dioxide and water vapour exchange over a temperate broad-leaved forest during the 1995 summer drought. Plant, Cell and Environment, 20, 1108-1122.

Baldocchi, D.D. & Harley, P.C. (1995). Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous gforest. II. Model testing and application. Plant, Cell and Environment, 18, 1157-1173.

Bartelink, H.H., Kramer, K. & Mohren, G.M.J. (1997). Applicability of the radiation-use efficiency concept for simulating growth of forest stands. Agricultural and Forest Meteorology, 88, 169-179.

Berry, J.A., Collatz, G.J., Denning, A.S., Colello, G.D., Fu, W., Grivet, C., Randall, D.A. & Sellers, P.J. (1997). SiB2, a model for simulation of biological processes within a climate model. p. 347-369. In P.R. van Gardingen, G.M. Foody & P.J. Curran, eds. Scaling-up: from cell to landscape. University Press, Cambridge. Source: Kruijt, B., Ongeri, S. & Jarvis, P.G. (1997).

Denmead, O.T. (1976). Temperate cereals. 1-32 p. In: J.L. Monteith (ed.) Vegetation and the atmosphere. Academic Press, London.

de Pury, D.G.G. & Farquhar, G.D. (1997). Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. Plant, Cell and Environment, 20, 537-557.

Edwards, N.T. & Hanson, P.J. (1996). Stem respiration in a closed-canopy upland forest. Tree Physiology, 16(4), 433-439. Source: Baldocchi, D.D. & Harley, P.C. (1995).

Goudriaan, J. (1982). Potential production processes. In: Penning de Vries, F.W.T. & Van Laar, H.H. (Eds) Simulation of plant growth and crop production. Simulation Monographs. Wageningen, Pudoc, 98-113 p. Source: Spitters, C.J.T. (1986).

Harley, P.C. & Baldocchi, D.D. (1995). Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. I. Leaf model parametrization. Plant, Cell and Environment, 18, 1146-1156.

Hollinger, D.Y. (1992). Leaf and simulated whole-canopy photosynthesis in two co-occurring tree species. Ecology, 73, 1-14. Source: Baldocchi, D.D. & Harley, P.C. (1995).

Johnson, D.W. & Henderson, G.S. (1989). Terrestrial nutrient cycling. 233-300 p. In: D.W. Johnson & R.I. van Hook, eds. Analysis of Biogeochemical Cycling Processes in Walker Branch Watershed. Springer-Verlag. New York. Source: Baldocchi, D.D. & Harley, P.C. (1995).

Kruijt, B., Ongeri, S. & Jarvis, P.G. (1997). Scaling of PAR absorption, photosynthesis and transpiration from leaves to canopy. p. 79-104. In P.R. van Gardingen, G.M. Foody & P.J. Curran, eds. Scaling-up: from cell to landscape. University Press, Cambridge.

Samson, R. Follens, S. & Lemeur, R. (1997). Scaling leaf photosynthesis to canopy in a mixed deciduous forest. I. Model Description. Silva Gandavensis-this issue.

Samson, R., Nachtergale, L., Schauvlieghe, M., Lemeur, R. & Lust, N. (1996). Experimental set-up for biogeochemical research in the mixed deciduous forest Aelmoeseneie (East-Flanders). Silva Gandavensis, 61, 1-14.

Spitters, C.J.T. (1986). Separating the diffuse and direct component of global radiation and its implications for modelling canopy photosynthesis. II. Calculation of canopy photosynthesis. Agricultural and Forest Meteorology, 38, 217-229.

Wang, K.Y. (1996). Canopy CO_2 exchange of Scots pine and its seasonal variation after four year exposure to elevated CO_2 and temperature. Agricultural and Forest Meteorology, 82, 1-27.

Wang, K.Y., Kellomäki, S. & Laitinen, K. (1995). Effects of needle age, long-term temperature and CO_2 treatments on the photosynthesis of Scotrs pine. Tree Physiology, 15, 211-218.

Wofsy, S.C., Goulden, M.L., Munger, J.W., Fan, S.-M., Bakwin, P.S., Daube, B.C. Bassow, S.L. & Bazzaz, F.A. (1993). Net exchange of CO_2 in a Mid-Latitude Forest. Science, 260, 1314-1317.