Quantification of the mutual relationships between forest growth and forest water use: determining factors, feedbacks and strategies

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5. COMPARISON OF DIFFERENT MODELING STRATEGIES FOR SIMULATING GAS EXCHANGE OF A DOUGLAS-FIR FOREST

ABSTRACT†

Carbon and latent heat fluxes can be simulated with different model strategies to fulfil different research purposes. In this study we compared four different model concepts: artificial neural networks (ANN), fuzzy logic (FL), an index model (IM, using light use efficiency and water use efficiency) and the process-based model FORGRO. The models were tested on a two-year data set of carbon and water fluxes of a Douglas-fir forest (Speuld, The Netherlands), one year before and one year after a thinning. The potentials of the model concepts for application for four research goals were assessed in relation to the obtained results and in a more general context: measurement fitting, insight into the importance of processes and mechanisms, simulation of climate change effects and upscaling of forest responses to regional scale.

For measurement fitting ANN and FL showed the highest potentials, mainly because of their high number of fitting parameters. IM and FORGRO showed a satisfactory model performance, although systematic errors were detectable. Insight into forest ecosystem functioning was difficult with ANN, but FL, IM and FORGRO showed clear interpretability of the effects of the thinning in terms of ecosystem functioning. FORGRO has the highest potentials for reliable estimation of effects of climate change on forests like Speuld, although the incorporation of adaptation to climate change in the model formulation is a major problem unsolved. For upscaling FL and ANN can be used effectively if they are parameterised on a range of forests rather than one forest as in this study. IM showed potentials for linking the model parameters to variables characterizing forest ecosystems like leaf area index, and thereby for large-scale applications. The discussion showed that the application of a set of totally different models can increase our knowledge of forest functioning.

INTRODUCTION

Models for simulating forest gas exchange, both carbon and latent heat, are developed for a range of application goals, for example carbon sequestration research, forestry and climate research (Medlyn et al., 1999; Williams et al., 1997; Mäkelä et al., 2000). Each application goal demands a certain level of process detail incorporated into the model. For large-scale climate models a simple model approach is necessary, because knowledge of species-specific parameter values is lacking in most cases (Williams et al., 1997). If one is interested in plant ecology and plant-physiological processes, the chosen model should probably include an elaborate light interception module, a soil module and a description

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of the photosynthesis and stomatal conductance characteristics of the studied species.

In most studies, models are developed and tested against measurements individually. A coherent comparison of the performance, obtained knowledge and application possibilities of different simulation models formulated and parameterised for the same measurements is rather seldom done, although for forest hydrology and transpiration models several comparisons have been performed (Bouten and Jansson, 1995; Barr et al., 1997; Garatuza-Payan et al., 1998; Bosveld and Bouten, 2000; Dekker et al., 2000a).

In this study we compare four different modelling strategies, which could be applied to simulation of gas exchange of a forest, both carbon and water fluxes. The forest is Douglas-fir forest in the central part of the Netherlands, for which two years (1995 and 1996) of eddy-covariance data of gas exchange are available (Bosveld, 1997; Bosveld and Bouten, 2000; Dekker et al., 2000a). In the winter of 1995 - 1996 a thinning took place in which one third of the trees was cut. An important criterion for the evaluation of the different models was how they could incorporate this thinning into their model formulations and/or model parameterisation.

The four strategies are a standard process-based forest-growth model, the FORGRO model (Mohren, 1987; Kramer and Mohren, 1996; Van Wijk et al., 2000a), artificial neural networks (ANN) (Van Wijk and Bouten, 1999), fuzzy logic (FL) (Van Wijk and Bouten, 2000a) and an index model (IM) based on the concepts of water and light use efficiencies (Van Wijk and Bouten, 2000b). All models are calibrated on carbon and latent heat fluxes. These four strategies were chosen because they vary strong in their use of deterministic knowledge, model structure and innovation, and because they are able to simulate both carbon and latent heat exchange.

The strategies were evaluated primarily on four aspects. First, model performance: how well did the models describe the measured data. Second, insight into the importance of processes and mechanisms: what kind of knowledge about the functioning of the forest ecosystem can be derived from the model. Third, the potentials for a reliable assessment of climate change effects and fourth, the application possibilities of the model techniques for upscaling of forest responses to regional scale.

**MATERIAL AND METHODS**

**Research site**
The study used data from a Douglas-fir stand of 2.5 ha within a large forested area (Speulderbos) near the village of Garderen, the Netherlands. The stand, which was planted in 1962, had a tree density of 780 trees ha⁻¹ and was without understory. Mean tree height between 1990 and 1992 was 21.6 m. Projected leaf area index ranged from 7.8 to 10.5 m² m⁻², which was estimated by needle samplings at different heights in different trees, and multiplying the measured
leaf densities by the tree density (Jans et al., 1994). The soil at Speuld is a Haplic Podzol, well drained, and consisting of fluvial deposits with textures ranging from fine sand to sandy loam. The groundwater-table is at 40 m. The 30-year mean rainfall is 834 mm year$^{-1}$. More detailed information on the research site has been published by Tiktak et al. (1988) and Van der Maas (1990).

**Measurements**

Meteorological conditions were measured by the Royal Meteorological Institute of the Netherlands (KNMI) from a 36 m tower. The types of measurement, the instruments and the data processing are described extensively in Bosveld (1997). Eddy covariance measurements of CO$_2$-fluxes in 1995 were performed with a DAT 300 sonic anemometer with a TR-61A probe (Kaijo Denki Co., Ltd., Tokyo, Japan) together with an open-path, infrared absorption sensor for latent heat and CO$_2$ (Kohsiek, 1991), mounted 30 m above the forest floor. CO$_2$-concentrations were measured at heights of 24 and 36 m with an LI-6262 infrared gas analyser (IRGA) (LI-COR, Inc., Lincoln, NE, USA). Nighttime CO$_2$-flux data were corrected for the effects of stable atmosphere and storage (Baldocchi and Vogel, 1996; Kimball et al., 1997) by also calculating nighttime CO$_2$-fluxes from CO$_2$-concentration profiles. The gradients flux was calculated with the turbulent exchange coefficient, which was assumed to be equal to the corresponding coefficient for the sensible heat flux; the latter was calculated according to Bosveld (1997). The time step of all measurements was 30 minutes. To avoid the influence of a neighbouring oak forest, data were removed from the data set when the wind was from the southwest. Latent heat (Lh) flux measurements within one day after a rainfall event were removed from the data set to prevent also simulating interception evaporation. In total there were 2093 CO$_2$-flux and 1490 latent heat flux measurements available in 1995, and 3823 CO$_2$-flux and 1879 latent heat flux measurements in 1996.

**Models**

FORGRO

FORGRO (FORest GROwth) (Mohren, 1987; Kramer and Mohren, 1996) is a process-based model suitable to predict growth of even-aged mono-species stands of trees. In the version presented in Van Wijk et al. (2000a), Van Wijk et al. (2000b) and Van Wijk and Bouten (2000a) FORGRO outputs may vary from instantaneous latent heat and carbon exchange to yearly forest yield and forest water use. Inputs of the model are global radiation ($R_g$), air temperature ($T$), wind speed, vapour pressure deficit (VPD) and precipitation.

Central to the process-based model FORGRO is the description of the attenuation of radiance in a canopy. The homogeneity of the canopy can be adjusted by increasing or decreasing the clustering factor that describes clustering of foliage around branches and within the canopy. The radiance intercepted by the canopy is weighted by the amount of foliage in each layer. Absorption of diffuse and direct fluxes of PAR (Photosynthetic Active Radiation) and NIR (Near Infrared Radiation), daily gross photosynthesis and transpiration are cal-
culated by integrating hourly over both sunlit and shaded leaf layers using a Gaussian integration scheme (Goudriaan and Van Laar, 1994).

The leaf photosynthesis module (Falge et al., 1996) is based on the approach of Farquhar and co-workers (Farquhar et al., 1980) using the model formulation of Harley and Tenhunen (1991). To calculate leaf photosynthesis and transpiration, we assumed that there were no gradients of CO₂, latent heat or temperature within the canopy; air temperature and humidity measured in the tower at 18 and 30 m showed no large systematic differences. The Leuning model was used to calculate the stomatal conductance (Leuning, 1995; Van Wijk et al., 2000a).

The costs of maintenance respiration are based on the costs of biosynthetic processes and the biochemical composition of structural biomass (Penning de Vries et al., 1974). Maintenance respiration depends on temperature according to a Q₁₀ approach, whereas growth respiration is assumed to be insensitive to changes in temperature (Goudriaan and Van Laar, 1994). Soil respiration rates were calculated with a model based on the concept of multiplicative interaction (Stroo et al., 1989; Freijer et al., 1996; Van Wijk et al., 2000a).

Artificial Neural Networks (ANN)
For a general non-linear mapping between the driving meteorological variables and the measured carbon and latent heat fluxes we used a standard three-layered back-propagation neural network. An artificial neural network gives the possibility for an 'unconstrained' non-linear fit which provides a benchmark against which more physically based models can be judged (Huntingford and Cox, 1997; Kosko, 1992; Demuth and Beale, 1998).

A three layer backpropagation neural network was used within Neural Network Toolbox 3.0 of Matlab 5.3 (Demuth and Beale, 1998). The optimisation method applied in the calibration phase was the Levenberg-Marquardt method. The total sum of squared errors (SSE) between measured and modelled values was minimised by tuning the artificial neural network parameters (e.g. scaling factors and inter-neuron connection weights). The number of epochs used in the optimisation was 75 and for each model fifty initialisations were tested. A model configuration with 3 hidden nodes showed to be the optimal configuration. With two hidden nodes the performance of the ANN decreased considerably, whereas the performance did not increase with more than three hidden nodes (Van Wijk and Bouten, 1999).

Global radiation, temperature and vapour pressure deficit were used as input variables. In an earlier analysis these variables were the most important driving variables for both the carbon fluxes as the latent heat fluxes (Van Wijk and Bouten, 1999).

Fuzzy Logic (FL)
Fuzzy logic is a mathematical tool that enables the representation of human decision and evaluation processes in algorithmic form. Fuzzy logic gives the possibility to model linguistic uncertainty by relating quantitative data to human logic expressions, like 'tall men', 'hot days', etceteras. These categories can then be
used for (complex) evaluations, like in human reasoning (Kosko, 1992; Zimmermann, 1996; Altrock, 1995). For example, ‘Tall men have large feet’.

A fuzzy logic model can be split up into three steps. In the first step, ‘normal’ quantitative data are translated into one or more linguistic classes. For example, if the fuzzy logic model input consists of one variable, for instance global radiation, the value of this variable is translated into the membership values of the defined classes. The membership-value can range from zero (does not belong to a certain class) to one (does totally belong to that class). This first step is called the ‘fuzzification’ step.

These calculated class memberships are then the input for the second step, the real model which consists of the fuzzy logic rules. Fuzzy logic rules are so-called ‘IF ... THEN ...’-rules. With these rules input-classes are coupled to output-classes, in our study the output-classes of the latent heat and carbon fluxes.

The third step is the so-called ‘defuzzification’ step, in which the memberships of the different classes of the output variables are translated into ‘normal’ quantitative data. These quantitative data are then the definitive output of the fuzzy logic model.

Both the fuzzification and the defuzzification step are dependent on the so-called membership functions and the class parameters. We used the most simple method of fuzzy logic: linear membership functions (Z-type, Lambda-type and S-type (Altrock, 1995) and centre of maximum defuzzification (Altrock, 1995; Zimmermann, 1996).

To be able to simulate fuzzy logic rules consisting of more than one input-variable we used the so-called Zadeh-operators. An example of a rule with more than one input is:

\[
\{\text{IF 'Radiation is High'}\} \ \text{AND} \ \{\text{IF 'Temperature is Middle-High'}\} \\
\ \ \ \ \ \text{THEN} \\
\ '\text{Latent Heat Flux is High'}
\]

The Zadeh-operators are (Kosko, 1992; Zimmermann, 1996; Altrock, 1995):

\[
\begin{align*}
\text{AND:} & \quad \mu_{A \land B} = \min \{\mu_A, \mu_B\} \\
\text{OR:} & \quad \mu_{A \lor B} = \max \{\mu_A, \mu_B\} \\
\text{NOT:} & \quad \mu_{\lnot A} = 1 - \mu_A
\end{align*}
\]

in which \(\mu\) is the membership value of the classes A and B, and \(\lnot\) is the logical ‘NOT’.

The model rules were calculated similar to Kosko (1992). First an initial guess of the different parameters was made. The model rules were derived by grouping the data into the different class-combinations of the three input variables. For each input class-combination the number of occurrences of a certain output class of the latent heat and carbon fluxes was calculated. The output class that was calculated most often for each input class-combination was then
defined as the model rule. For a more thorough introduction to the Fuzzy Logic method as applied in this study, see Van Wijk and Bouten (2000a).

Index Model (IM)
The index-model used is based on the concepts of the RESCAP-model presented in Dewar (1997). The only adaptation was replacing the linear relation between radiation and growth by a curve-linear relation between radiation and assimilation (Van Wijk and Bouten, 2000b). The carbon flux is divided into an assimilation-term, which we assume radiation driven, and a respiration term, which we assume temperature driven. The assimilation relation is given by a saturated curve-linear relation:

\[ Ass = \frac{a \cdot R_g}{b + R_g} \]  

(1)

In which:
- \( R_g \) is global radiation (expressed in MJ m\(^{-2}\) d\(^{-1}\))
- \( Ass \) is radiation driven canopy assimilation (expressed in g CO\(_2\) m\(^{-2}\) d\(^{-1}\))

Interpretation of parameters: ‘a / b’ is the initial light use efficiency of the forest canopy (in g CO\(_2\) MJ\(^{-1}\)), and ‘a’ is the saturated, or maximum, canopy assimilation (in g CO\(_2\) m\(^{2}\) d\(^{-1}\)).
- ‘b’ is in MJ m\(^{2}\) d\(^{-1}\)

This formulation of the relationship is chosen because the simple conceptual interpretation of the two coefficients.

The respiration relation:

\[ R = c \cdot 2^{(T/25 - 10)} \]  

(2)

In which:
- ‘R’ is the forest respiration (in g CO\(_2\) m\(^{2}\) d\(^{-1}\)), ‘c’ is the reference respiration at 25°C (in g CO\(_2\) m\(^{2}\) d\(^{-1}\)) and ‘T’ is temperature in °C

For the relation between assimilation and transpiration we used the VPD-correction as shown in the appendix of Dewar (1997):

\[ T = \frac{1}{q_0} \cdot Ass \cdot \left( \frac{1}{D} + \frac{1}{D_0} \right)^{-1} \]  

(3)

In which:
- ‘T’ is transpiration (in mm H\(_2\)O d\(^{-1}\)), ‘\( q_0 \)’ is the VPD corrected water use efficiency (in g CO\(_2\) kg H\(_2\)O\(^{-1}\) kPa), ‘D’ is vapour pressure deficit (in kPa) and ‘D\(_0\)’ is an empirical constant (in kPa)
These units were used in Van Wijk and Bouten (2000b). In this paper the results were calculated into $\mu$mol m$^{-2}$ s$^{-1}$ for the carbon fluxes and W m$^{-2}$ for the latent heat fluxes to make a comparison possible with the simulation results of the other models.

**Model calibration and sensitivity analysis**

All models were parameterised on the two years of available data of latent heat and carbon exchange, and the meteorological driving variables. The number of adapted model coefficients to incorporate the thinning, or the number of fit-parameters used to calibrate the models onto the available data are given in Table 1. The thinning event was incorporated into the FORGRO model by decreasing the LAI from 7 m$^2$ m$^{-2}$ to 4 m$^2$ m$^{-2}$ and doubling the cluster factor (Van Wijk and Bouten, 2000a; Van Wijk et al., 2000b).

The ANN's were trained on the two years of data separately. This training was performed on 50% of the data of each year, randomly selected from the total data sets. After this training a sensitivity analysis was applied to the resulting ANN's as in Huntingford and Cox (1997) and Van Wijk and Bouten (1999). In this analysis each input variable, in our case radiation, temperature and vapour pressure deficit, was varied from the lowest to the highest measured value. Together with the mean values of the other inputs the neural network outcome was calculated. With these results three plots were obtained in which a different input variable was analysed. The training and the subsequent sensitivity analysis were performed twenty times on a new randomly selected training set. By this multiple training the consistency of the relations found can be tested (Schaap and Leij, 1998).

Both the FL-rules and the FL-class parameters were derived and optimised for the two years independently, similar to Van Wijk and Bouten (2000a). The rules and the parameter of 1995 and 1996 were compared and differences were interpreted.

IM-parameters were optimised using the Simplex-optimisation (Press, 1989), also for both years separately. After this optimisation a parameter sensitivity analysis was performed to test whether the shifts that were found in the optimised values of the different parameters were real changes in ecosystem efficiencies or only small changes in an uncertain parameter space (Van Wijk and Bouten 2000b). In the analysis IM was run with 50 values of each parameter. All model parameterisations with a performance within two times the standard deviations of the half-hourly fluxes were accepted as reasonable performing parameter combinations. To perform this analysis we had to define measurements outside the uncertainty intervals as outliers. The outlier amounts were about 30 measurements, only a very small part of the total data set. The accepted parameter values of 1995 and 1996 were plotted in the same graphs to evaluate the parameter shifts (Van Wijk and Bouten, 2000b).
Table 1: Number of adjusted parameters (in the case of FORGRO) and the number of fit parameters (in the cases of Artificial Neural Networks (ANN), Fuzzy Logic (FL) and the Index Model (IM)) to describe the two years of available data

<table>
<thead>
<tr>
<th>Model</th>
<th>Number of parameters</th>
<th>Description of parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>FORGRO</td>
<td>2</td>
<td>Leaf Area Index</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cluster coefficient</td>
</tr>
<tr>
<td>ANN</td>
<td>16 + 16 (carbon and water flux separately)</td>
<td>Fit-parameters</td>
</tr>
<tr>
<td>FL</td>
<td>17 + 17 (carbon and water flux separately)</td>
<td>Fit-parameters</td>
</tr>
<tr>
<td>IM</td>
<td>5</td>
<td>Fit-parameters</td>
</tr>
</tbody>
</table>

RESULTS

Model performance
The performances of different models are given in Table 2, expressed in normalised root mean square error (NRMSE) (Janssen and Heuberger, 1995) and the explained variance ($R^2$). For all four sets of measurements available, the carbon fluxes of 1995 and 1996 and the Lh-fluxes of 1995 and 1996, the ANN's showed the highest performance of all models, expressed in both error measures. The FORGRO-model had the lowest performance in simulating the carbon fluxes, whereas the performance in simulating the Lh-fluxes is comparable to IM. The FL-models performed almost similar to the ANN's, except for the carbon fluxes of 1995 where the NRMSE of FL was clearly higher than that of ANN.

In Figure 1 latent heat and carbon flux measurements of one day of each year (not the same days because of missing data) are plotted together with the typical simulation results of the different models. These days were chosen because typical differences between the simulated values of the models were present. For the 1995 Lh-fluxes there were no large systematic differences between the models, whereas in 1996 both FORGRO and the IM over-estimated the Lh-fluxes at high levels of VPD. For the carbon fluxes of 1995 and 1996 both FORGRO and IM over-estimated the fluxes in the late afternoon–early evening. FL had the same systematic error in 1995. In 1996 also during the day a clear difference was visible between the FORGRO and IM on one side and FL and ANN on the other. This difference was related to high VPD values: during this day VPD reached a value of 25 hPa. Both FL and ANN decreased their carbon uptake related to these high values whereas FORGRO and the IM showed no response.
Table 2: Model performances for the two years of CO₂ and latent heat flux data, expressed in normalised root mean square error (NRMSE), R² between brackets

<table>
<thead>
<tr>
<th></th>
<th>ANN</th>
<th>Fuzzy Logic</th>
<th>Index Model</th>
<th>FORGRO</th>
</tr>
</thead>
<tbody>
<tr>
<td>CO₂ 1995</td>
<td>1.86 (0.79)</td>
<td>1.92 (0.78)</td>
<td>2.04 (0.76)</td>
<td>2.16 (0.73)</td>
</tr>
<tr>
<td>CO₂ 1996</td>
<td>1.82 (0.59)</td>
<td>1.83 (0.62)</td>
<td>1.93 (0.58)</td>
<td>2.00 (0.56)</td>
</tr>
<tr>
<td>Water vapour 1995</td>
<td>0.36 (0.88)</td>
<td>0.37 (0.88)</td>
<td>0.40 (0.87)</td>
<td>0.41 (0.86)</td>
</tr>
<tr>
<td>Water vapour 1996</td>
<td>0.46 (0.83)</td>
<td>0.47 (0.82)</td>
<td>0.55 (0.77)</td>
<td>0.54 (0.80)</td>
</tr>
</tbody>
</table>

Response curves of the optimised ANN-models

In Figure 2 the response curves are plotted of all 20 sets of the four ANN-models. The response curves of the two Lh-flux ANN's were clearly different. The 1996-curves were lower than the 1995 curves, reflecting a decrease in transpiration caused by the thinning. However, no clear differences between 1995 and 1996 were present in the qualitative relations between the Lh-flux ANN-responses and varying radiation and temperature inputs. The levelling off of the ANN response to VPD seems to be taking place at lower values of VPD in 1996 than in 1995, although this interpretation is hampered by the high uncertainty of the response curves. These changes in the ANN-response to VPD could reflect an increased sensitivity to VPD of the forest canopy.

Figure 1: Typical simulated and measured values of the 1995 and 1996 CO₂ and latent heat fluxes
The radiation-responses of 1995 carbon ANN-model showed a larger effect of radiation than the 1996 ANN-model: at low radiation levels there was a slightly higher positive carbon flux, i.e. more respiration in the dark, and more negative carbon fluxes at high radiation levels, i.e. more carbon uptake at day-time. This difference also reflected the effect of the thinning: because of the strong decrease in biomass present in 1996 compared to 1995, less respiration occurred, but also the amount of assimilation decreased. The sensitivity analysis for the carbon ANN's revealed a larger effect of temperature on the ANN-models in 1996: the slope of the 1996 response curves was more negative than of the 1995 response curves. Especially the 1996 response showed that according to

Figure 2: Response curves of artificial neural networks for CO$_2$ and latent heat fluxes of 1995 and 1996
the ANN the positive effect of an increased temperature on assimilation is larger than the positive effect of temperature on respiration: the net carbon uptake by the forest increases at higher temperatures. In the carbon response curves the increased effect of VPD on the simulated fluxes in 1996 was more clearly visible than it was for the latent heat flux ANN. At high VPD-values the carbon fluxes of 1996 were less negative than in 1995, probably reflecting an increased down-regulation of the stomatal conductance at high VPD-values and thereby decreasing the carbon uptake due to assimilation.

It is important to keep in mind while interpreting these figures, that when one input was varied the other inputs were kept at their mean value. In this way the correlations that are always present in the measured inputs, for example high VPD with high radiation, are broke through in the ANN-responses. In this way effects of VPD can be distinguished from effects of temperature of radiation, although the responses of ANN should always be interpreted with some care.

**Fuzzy Logic rules and parameters**

In Table 3 and 4 the parameters and rules of the four different FL-models are given. The parts of Table 4 are divided into four blocks, each representing one VPD input class. Within each block the rows represent the global radiation input classes, and the columns represent the temperature input classes. The numbers that are given for each combination of global radiation, temperature and VPD input classes are the derived FL output rules for the Lh-fluxes. For example, the most upper right number of the second (from the left) VPD-block (in italic and underlined), of which the value is one, represents the FL rule:

{IF 'Rg is LOW'} AND {IF 'T is HIGH'} AND {IF 'VPD is LOW-MIDDLE'}

THEN

' Lh-flux is LOW''

A detailed discussion of the rules of the Lh-flux FL-model can be found in Van Wijk and Bouten (2000b). The most interesting result of the Lh-flux models was the clear difference in the rules derived at the Middle-High and High VPD-classes. In the rules of FL 1996 a down-regulation was present when the rules of the VPD-inputs Middle-High and High are compared at the higher temperature and radiation inputs (see Table 4A, italic rules). This effect was not present in the 1995 rules. Also a decrease in the occurrence of the highest flux class was visible in 1996 compared to 1995, representing the decrease in transpiration after the thinning.

The most important differences between the rules of the 1995 and 1996 carbon models occurred at the Middle-High radiation inputs, with higher classes in 1996 compared to 1995, meaning less carbon uptake by the forest. The expected decrease in ecosystem respiration due to the thinning was not represented clearly in the rules but was present in the difference in the highest class-parameter of the carbon fluxes. The highest class-parameter of the 1995 carbon fluxes was 7.0 µmol m$^{-2}$ s$^{-1}$, whereas the 1996 parameter was 5.2 µmol m$^{-2}$ s$^{-1}$ (see Table 3b). The 1995 and 1996 carbon models also differ at the highest VPD input, but these changes were less easy to link to the thinning.
Table 3: Parameters (initial guess, 1995-optimised and 1996-optimised) of the latent heat (a) and CO\textsubscript{2} (b) flux fuzzy logic model

### A

<table>
<thead>
<tr>
<th></th>
<th>Class I</th>
<th></th>
<th></th>
<th>Class II</th>
<th></th>
<th></th>
<th>Class III</th>
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<td>Initial</td>
<td>'95</td>
<td>'96</td>
<td>Initial</td>
<td>'95</td>
<td>'96</td>
<td>Initial</td>
<td>'95</td>
<td>'96</td>
</tr>
<tr>
<td>Rg [W m\textsuperscript{-2}]</td>
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<td>-2.6</td>
<td>10.7</td>
<td>100</td>
<td>130</td>
<td>168</td>
<td>500</td>
<td>779</td>
<td>388</td>
<td>900</td>
<td>937</td>
<td>744</td>
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<td></td>
<td></td>
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<tr>
<td>T [°C]</td>
<td>0</td>
<td>-</td>
<td>0.7</td>
<td>7.5</td>
<td>10.2</td>
<td>12.2</td>
<td>15.0</td>
<td>11.6</td>
<td>17.3</td>
<td>25.0</td>
<td>18.5</td>
<td>19.3</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>VPD [hPa]</td>
<td>0</td>
<td>0.5</td>
<td>2.2</td>
<td>7.5</td>
<td>0.6</td>
<td>2.2</td>
<td>15.0</td>
<td>6.7</td>
<td>10.8</td>
<td>25.0</td>
<td>29.4</td>
<td>23.6</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Lh [W m\textsuperscript{-2}]</td>
<td>0</td>
<td>4.2</td>
<td>3.0</td>
<td>40</td>
<td>23.6</td>
<td>43.1</td>
<td>80</td>
<td>69.4</td>
<td>70.2</td>
<td>120</td>
<td>80.0</td>
<td>97.9</td>
<td>165</td>
<td>202</td>
<td>185</td>
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### B

<table>
<thead>
<tr>
<th></th>
<th>Class I</th>
<th></th>
<th></th>
<th>Class II</th>
<th></th>
<th></th>
<th>Class III</th>
<th></th>
<th></th>
<th>Class IV</th>
<th></th>
<th></th>
<th>Class V</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Initial</td>
<td>'95</td>
<td>'96</td>
<td>Initial</td>
<td>'95</td>
<td>'96</td>
<td>Initial</td>
<td>'95</td>
<td>'96</td>
<td>Initial</td>
<td>'95</td>
<td>'96</td>
<td>Initial</td>
<td>'95</td>
<td>'96</td>
</tr>
<tr>
<td>Rg [W m\textsuperscript{-2}]</td>
<td>0</td>
<td>-1.5</td>
<td>-13.1</td>
<td>100</td>
<td>113</td>
<td>123</td>
<td>500</td>
<td>607</td>
<td>443</td>
<td>900</td>
<td>1182</td>
<td>7.5\textsuperscript{15}</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T [°C]</td>
<td>0</td>
<td>-2.9</td>
<td>0.1</td>
<td>7.5</td>
<td>2.8</td>
<td>10.1</td>
<td>15.0</td>
<td>13.6</td>
<td>11.0</td>
<td>25.0</td>
<td>14.3</td>
<td>13.4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VPD [hPa]</td>
<td>0</td>
<td>2.8</td>
<td>0.6</td>
<td>7.5</td>
<td>5.6</td>
<td>1.6</td>
<td>15.0</td>
<td>7.8</td>
<td>11.2</td>
<td>25.0</td>
<td>32.3</td>
<td>21.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lh [W m\textsuperscript{-2}]</td>
<td>-15.0</td>
<td>-20.3</td>
<td>-18.4</td>
<td>-10.0</td>
<td>-4.0</td>
<td>-11.3</td>
<td>5.0</td>
<td>-2.9</td>
<td>-4.2</td>
<td>0.0</td>
<td>0.2</td>
<td>-0.4</td>
<td>5.0</td>
<td>7.0</td>
<td>5.2</td>
</tr>
</tbody>
</table>

Rg is global radiation, T is temperature, VPD is vapour pressure deficit and Lh is latent heat flux
Table 4: Calculated fuzzy logic rules for the latent heat (a) and CO₂ (b) fluxes of Speuld 1995 and 1996 using initial guess parameters of table 3a and b (1 = low, 2 = low-middle, 3 = middle, 4 middle-high, 5 = high)

### A

#### Speuld 1995

<table>
<thead>
<tr>
<th>VPD low</th>
<th>VPD low-middle</th>
<th>VPD middle-high</th>
<th>VPD high</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Rg/ T</strong></td>
<td><strong>L</strong></td>
<td><strong>m-l</strong></td>
<td><strong>m-h</strong></td>
</tr>
<tr>
<td><strong>L</strong></td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>m-l</strong></td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td><strong>m-h</strong></td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td><strong>h</strong></td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
</tbody>
</table>

### B

#### Speuld 1995

<table>
<thead>
<tr>
<th>VPD low</th>
<th>VPD low-middle</th>
<th>VPD middle-high</th>
<th>VPD high</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Rg/ T</strong></td>
<td><strong>L</strong></td>
<td><strong>m-l</strong></td>
<td><strong>m-h</strong></td>
</tr>
<tr>
<td><strong>L</strong></td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>m-l</strong></td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td><strong>m-h</strong></td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td><strong>h</strong></td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
</tbody>
</table>

#### Speuld 1996

<table>
<thead>
<tr>
<th>VPD low</th>
<th>VPD low-middle</th>
<th>VPD middle-high</th>
<th>VPD high</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Rg/ T</strong></td>
<td><strong>L</strong></td>
<td><strong>m-l</strong></td>
<td><strong>m-h</strong></td>
</tr>
<tr>
<td><strong>L</strong></td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>m-l</strong></td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td><strong>m-h</strong></td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td><strong>h</strong></td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
</tbody>
</table>

Rg is global radiation. T is temperature. VPD is vapour pressure deficit; l is Low, m-l is Middle-Low, m-h is Middle-High and h is High.
Table 5: Parameter values of the Index Model (for explanation of the symbols see text)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value for 1995</th>
<th>Value for 1996</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Assimilation</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$a$ [g CO$_2$ ha$^{-1}$ s$^{-1}$]</td>
<td>18.6</td>
<td>10.6</td>
</tr>
<tr>
<td>$b$ [W m$^{-2}$]</td>
<td>439.3</td>
<td>216.4</td>
</tr>
<tr>
<td>$a / b$ [g CO$_2$ MJ$^{-1}$]</td>
<td>4.2</td>
<td>4.9</td>
</tr>
<tr>
<td><strong>Respiration</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$c$ [g CO$_2$ ha$^{-1}$ s$^{-1}$]</td>
<td>4.8</td>
<td>3.5</td>
</tr>
<tr>
<td><strong>Transpiration</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WUE [g CO$_2$ kg H$_2$O$^{-1}$]</td>
<td>3.4</td>
<td>3.0</td>
</tr>
<tr>
<td>$D_0$ [kPa]</td>
<td>0.26</td>
<td>0.23</td>
</tr>
</tbody>
</table>

Figure 3: Accepted parameter values of the Instantaneous Model of 1995 and 1996 (for explanation see text); the coefficient not shown in the diagrams of the CO$_2$ part of the model is at its optimal value, see Table 5.
Parameters of the Index Models (IM)
The parameters of IM are presented in Table 5: the optimised values of the coefficients showed clear differences between 1995 and 1996. However, when the results of the sensitivity analysis (see Figure 3) were taken into account, there was no systematic change in the water use efficiency parameter and the VPD-coefficient. There was for all parameters a clear correlation visible between the accepted values. The shifts in the 'a', 'b' and 'c' parameters of the carbon part were significant. The changed parameter-values represent a decrease in respiration and a decrease in the radiation saturated assimilation due to the thinning.

DISCUSSION

Measurement fitting
If one looks only at the performance of the models then the ANN's were the best models. This is of course not surprising: the main reason for applying ANN is always their high performance in input-output fitting (Lek and Guegan, 1999). The second best performing modelling technique was FL. FORGRO and IM showed a comparable performance. This follow up of model performances is strongly coupled to the number of fitting parameters used in the different approaches, see Table 1. The FORGRO-version has only two adapted parameters, the leaf area index and the clustering factor (Van Wijk et al., 2000b) and therefore the lower performance was not surprising. This low number of fit-parameters can also be seen as an advantage of the FORGRO-model. ANN, FL and IM need a difficult parameter-optimisation, and are highly empirical, whereas the FORGRO-model can be tested thoroughly on the measured data, because the parameterisation of the model was done almost independently of the validation data.

However, this comparison of the number of fit-parameters is not completely fair because in FORGRO a very high number of species-specific parameters are also present, especially in the leaf photosynthesis model of Farquhar. These parameters are not fitted on the data that are used here for the evaluation, and therefore not considered as 'fit'-parameters. The IM-model has also potentials for species-specific parameterisation, especially for the Water Use Efficiency (WUE) and the initial light use efficiency (see discussion below, in 'Insight in importance ...'). This independent parameterisation of the more physiological interpretable parameters of IM would of course strongly decrease the number of fit-parameters, and thereby increase the application possibilities.

Insight in importance of different processes and mechanisms (how does the system work?)
The four model concepts showed clear differences. The detailed process-based model FORGRO is excellent as a summary of current knowledge of forest functioning. It integrates the main processes of the compartments tree and soil, and gives thereby the possibility to test the interactions of the biotic and abiotic
components in the forest ecosystem. However, because this type of model integrates all our current knowledge about the processes working in forest ecosystems, the applications to the two different years does not produce really new insights by itself. The model is too complex to judge whether the differences between 1995 and 1996 can also be represented by adjusting other parameters than the LAI and the clustering factor. The adjustment was purely made on the basis of the knowledge of the forest already present, and not determined by the data.

A clear disadvantage of ANN is the fact that they are, in principle, black boxes. Different methods are used for the so-called 'elucidation' of ANN. A simple method is the sensitivity analysis as applied in this study. The interpretation of these response-curves is hampered by the correlation between especially the temperature and VPD inputs: this means that it will be difficult for a correlative technique like ANN, which has no pre-defined model, to distinguish between the effects of these variables. Another disadvantage is the fact that an input can only be evaluated by keeping the other inputs at a constant value. The responses therefore only give a limited view of the potential complex interactions present in the derived ANN's.

Especially FL and IM give new insights in forest functioning, and the changes that occurred in forest functioning due to the thinning. The rules of FL can be interpreted directly because the rules are based on human reasoning, and the linkage to ecosystem functioning is relatively easy. For example, the increased effect of VPD on the down-regulation of evapotranspiration was easy to detect when the rules of the 1995 and 1996 models were compared. In this way FL can give an easy interpretable summary of the responses present in the data. The parameters were less easy to interpret because of interrelationships between class values of one variable with class values of another variable. Only the upper and lower class values (the 'High' and 'Low'-classes) showed clear interpretability (Van Wijk and Bouten, 2000a).

The changes of parameters of IM due to the thinning showed potentials for linkage to ecosystem properties. The coefficients that did not change, 'q₀' (water use efficiency), 'D₀' and 'a/b' (initial light use efficiency), can be considered as more physiologically determined by their definition. The water use efficiency and initial light use efficiency are more species intrinsic coefficients, and less affected by management than the saturated assimilation coefficient. In this way the parameters of the model can be separated into parameters that can be determined by using species characteristics and by parameters that can be determined by using stand characteristics (Van Wijk and Bouten, 2000b). Both the saturated assimilation and the respiration coefficient are influenced by the amount of foliage present. Both coefficients decreased from 1995 to 1996 with a similar factor as the foliage: almost one-third. Of course, the IM should also be tested on other forests to determine whether the linkage between Leaf Area Index and the model parameters is generally applicable.

An important outcome of this study is the fact that the combination of several models applied to the same data gives a clear increase in our insight in forest functioning. FORGRO and IM both had systematic errors present in model-
ling of the carbon fluxes and the 1996 Lh-fluxes. On the basis of the same inputs these systematic errors were not present in the FL and ANN-models. This is therefore a trigger to search for the cause of this difference between the different models. For this search FL can be used because of the interpretable rules. ANN can be used to analyse the model mismatch as has been done in Dekker et al. (2000b).

For the latent heat fluxes both FORGRO and IM showed an overestimation at high VPD values. The increased effect of VPD on the down-regulation of the evapotranspiration, as clearly shown in the derived FL rules, and only slightly visible in the response curves of the 1996 ANN, could not be represented by both models. For FORGRO this means that not all changes in forest-ecosystem functioning could be incorporated by increasing the clustering factor. Incorporation of canopy-atmosphere exchange coefficient is probably necessary to simulate the stronger coupling between the canopy and the atmosphere, due to the more open canopy as a side-effect of the thinning (Van Wijk and Bouten, 2000a). By increasing the exchange of water vapour, the canopy and the atmosphere the thinning effect can be represented better. In the version of FORGRO used in this article no gradients of humidity in the canopy were assumed (Van Wijk et al., 2000a).

FL-model outcomes were similar to those of ANN (see Figure 1), although the carbon model of 1995 slightly over-estimated the net carbon fluxes at the beginning of the night. This effect however was rather small, and was not visible for the 1996 model, whereas both FORGRO and IM showed this model mismatch for both 1995 and 1996. This could be both a model-error, the respiration-temperature relation is not correct, or a measurement problem, there could be a storage effect present in the carbon fluxes which leads to a delay in the flux responses to changes in the environment (Baldocchi and Vogel, 1996). As both ANN and FL are fitted on the measurements with a high number of fitting parameters it is possible that these two methods have incorporated this storage effects in their input-output relations, whereas both FORGRO and IM, which are defined from a more process-based viewpoint, have not.

Simulation of climatic change scenarios
One of the most important reasons to develop process-based models is their potential for application outside the interval of current available climate data. Models based on concepts like ANN, IM and FL, are fitted on the available micro-meteorological data above forest ecosystems. Therefore, they are not reliable outside the range of available measurements. Physiologically based models like FORGRO however, are parameterised using data of lower-level processes, like leaf photosynthesis and respiration. These measurements can be extended outside the boundaries of current climate relatively easy, for example in experiments with increased CO₂-concentrations (Medlyn et al., 1999). A major problem with these experiments however is that they are in most cases short term, and cannot incorporate all the interactive reactions and adaptations that a tree exhibits during its long lifetime (Idso, 1999). This can therefore lead to over-estimation of the effects of climate change (Rastetter, 1996).
For example, both the photosynthesis and respiration relations in the Farquhar model are determined by fixed parameters like $V_{cmax}$ (maximum carboxilation speed), $J_{max}$ (quantum use efficiency) and $C_{resp}$ (respiration coefficient) (Harley and Tenhunen, 1991; Farquhar et al., 1980). However, these coefficients change due to physiological adaptation of the plant. Research showed that the photosynthetic parameters change when plants are subjected to changes in carbon dioxide concentration (Medlyn et al., 1999; Rastetter, 1996). There is experimental evidence that the adaptation of the photosynthesis coefficients in small trees can be linked to changes in leaf nitrogen concentration, but this of course shifts the problem to the correct prediction of leaf nitrogen under climate change (Medlyn et al., 1999). Respiration in the current formulation in the Farquhar model is highly sensitive to temperature, and there are indications for adaptation of this sensitivity at changing temperatures (Dewar et al, 1999). Other research showed a down-regulation of respiration at increased atmospheric carbon concentrations (Tjoelker et al., 1999; Drake et al., 1999). Application of these models for climate change, which is always used as an important argument for the development of the process-based models, is therefore not reliable at the moment, or at best only qualitatively reliable. Future developments must incorporate possibilities for adaptation of parameter-values due to changing environments. A question that is still unanswered, is whether that will be possible within these already complex process-based models.

**Upscaling of forest responses to regional scale**

A related application goal to the previously described one is the question of up-scaling of local responses to regional scale. In this discussion the term ‘regional’ is used at a maximum scale of about 50 by 50 km, so that climatic difference within the region can be ignored in most cases. Budgeting the global C cycle and the contributions of separate regions in the world to the storage of carbon in ecosystems are important issues in current science (Luo and Mooney, 1995). Applications of simulation models are essential for reliable descriptions of the global C cycle. The type of simulation models that is used can also be critical for the outcomes of such an analysis. How much biological process knowledge must be incorporated into the models to include forest responses at higher spatial scales? Another important aspect is how easy models parameterised for one forest location can be applied with more or less confidence for other forest locations. For example, if the goal is to develop a regional GIS-model to describe carbon and water exchange, it will be essential that models that are tested for a per definition limited number of locations can be applied with confidence for the rest of the region.

For a successful application of lower-scale models to other forests the inclusion of generally applicable relations and responses is essential. The processes included in FORGRO are universal for all forests and the model has the potential for general application. On the other hand, this potential for general application by including the main processes of all the forest compartments also leads to their main disadvantage: the complexity of process-based models like FORGRO. Each process that is simulated by the model needs a set of parameters and the
total model therefore needs a huge amount of parameterisation. At the moment this can only be achieved for single forest locations, which are studied thoroughly for many years and where large scientific research teams are collaborating. It will be an illusion to expect a reliable large-scale application of these models for all different kinds of forest sites in the near future. The main improvements to increase the application possibilities for the FORGRO-kind of models are achieved by relating the Farquhar-photosynthesis parameters to leaf-nutrients (Medlyn et al., 1999). This gives an opportunity for model simplification as is done by Williams et al. (1997), although not for all species the leaf photosynthetic – leaf nutrient relations are available at the moment. However, the greatest problem will be a simple representation of respiration. There are probably no simple indicators present to link forest ecosystem respiration to. Leaf respiration is strongly coupled to leaf-nutrients, but the soil compartment, which is important in the ecosystem respiration, is difficult to characterize apart from direct measurements.

Application of an ANN derived for one forest as is done in this study to other forest sites is difficult. ANN is an empirical technique and is, also because of its non-linearity, sensitive to extrapolation. As the parameters of a trained ANN are difficult to interpret into terms of ecosystem functioning they cannot be adjusted in a simple way for other forest ecosystems on the basis of expert knowledge. To apply an ANN to other forests not used in the parameterisation successfully, the ANN should have been trained on several forest location differing in species, leaf area index, nutrient availability, etceteras, as has been done in Van Wijk and Bouten (1999). This ANN can be used for other forests, because the other forests are then interpolations between the forests that are used in the training of the ANN. For such an application ANN is very powerful, because once an ANN is trained it is very fast in its application. The same reasoning can be applied to FL, see Van Wijk and Bouten (2000a). A clear drawback of this empirical approach is of course the fact that a huge amount of data is necessary for such an application.

An advantage of IM and FL compared to ANN is their open model structure, which gives potentials for expert based model adjustment: rules and parameters are much easier to interpret than the matrix coefficients of ANN. The IM further showed clear potentials for linking model parameters to functional ecosystem properties like the leaf area index (Van Wijk and Bouten, 2000b). When these ecosystem properties are easy to measure this would make large application possible. If also for each species the more physiologically interpretable parameters of IM, like WUE and the initial light use efficiency, can be determined and used generally for a certain species, IM clearly has very good potentials for large-scale applications.
CONCLUSIONS

After applying the model techniques to a two year dataset of Speuld, they were evaluated on four aspects: model performance, insight into the importance of processes and mechanisms, the potentials for a reliable assessment of climate change effects and fourth, the application possibilities of the model techniques for upscaling of forest responses to regional scale.

For measurement fitting ANN and FL showed the highest potentials, mainly caused by their high number of fitting parameters. IM and FORGRO showed a satisfactory model performance, although systematic errors were detectable. To get insight into forest ecosystem functioning was difficult with ANN, but FL, IM and FORGRO showed clear interpretability of the effects of the thinning in terms of ecosystem functioning. FORGRO has the highest potentials for reliable estimation of effects of climate chance on forests like Speuld, although the incorporation of adaptation to climate chance in the model formulation is still a major problem unsolved. For upscaling FL and ANN can be used effectively if they are parameterised on a range of forests rather than one forest as in this study. IM showed potentials for linking the model parameters to variables characterizing forest ecosystems like leaf area index, and thereby for large-scale applications, but for this the model should be tested on a range of forests. FORGRO by itself is too complex for upscaling, although its generally applicable forest responses can be used to derive simplified model formulations. The integral comparison of totally different modelling techniques applied to the same data set can increase our knowledge of forest functioning.

REFERENCES


Van Wijk, M.T., Bouten, W., 2000b. Simulating daily and instantaneous forest carbon and water exchange with a simple model of light and water use. Submitted to Tree Physiology. Chapter 3 of this thesis.


