Quantification of the mutual relationships between forest growth and forest water use: determining factors, feedbacks and strategies
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3. SIMULATING DAILY AND HALF-HOURLY FLUXES OF FOREST CARBON AND WATER VAPOUR EXCHANGE WITH A SIMPLE MODEL OF LIGHT AND WATER USE†

ABSTRACT

A simple light and water use model was used to simulate half-hourly and daily carbon and water exchange of a Douglas fir forest (*Pseudotsuga menziesii* (Mirb.) Franco) in the Netherlands for two years, before and after a thinning. The model divides carbon-fluxes into a radiation driven assimilation term and a temperature driven respiration term. Water exchange is simulated using the simulated assimilation term, vapour pressure deficit and a water use efficiency coefficient. The performance of the half-hourly model was satisfactory and similar to the performance of the process-based model FORGRO, whereas the performance of the daily model was high for water exchange, but clearly lower than FORGRO for carbon exchange. Comparison of the model parameters before and after the thinning showed that the coefficients of the half-hourly model could be separated into more physiologically determined and stand determined characteristics, whereas for the daily model this separation was not clear, probably because of non-linear aggregation effects. These results indicate that the half-hourly model has potential for large scale application by relating ecosystem characteristics like the leaf area index to model coefficients. A sensitivity analysis showed that strong correlations exist between similar performing parameter-sets. For comparison of parameter values of different studies, even for these simple models, ranges of parameter values and their correlations should be presented rather than the optimised values.

INTRODUCTION

At the moment the up-scaling of carbon and water fluxes from forest canopy scale to regional scales is an important issue (Jarvis 1995, Dewar 1997, Williams et al. 1997). Fine-scale process-based models that use physiological knowledge about carbon and water exchange at leaf level (Farquhar et al. 1980) are commonly used to simulate carbon and water exchange at canopy level (for example Wang and Jarvis 1990, Williams et al. 1996, Falge et al. 1997). However, application of these models at regional scale is hampered by the need of physiological and site-specific parameters, like leaf photosynthesis and respiration characteristics, soil parameters, etceteras. Another problem is the large amount of input data needed for model runs (Williams et al. 1997). A promising way to overcome these problems is the derivation of simplified versions of the fine-scale

† Submitted by M.T. van Wijk and W. Bouten to Tree Physiology. © Heronpublishing
models, in which only the most important and easy measurable driving variables are included. Williams et al. (1997) is a good example of simplification of a complex fine-scale model into a much simpler broad scale model, although their broad scale model still needs difficult to obtain empirical knowledge about water pressure head differences between the soil and plant compartment.

Another approach is the use of simple relations of growth and water use emerging at canopy scale. The most important concepts used are a linear relation between the amount of dry matter produced and the amount of intercepted radiation, expressed as the light or radiation use efficiency (Bartelink et al. 1997, Dewar 1997), and a linear relation between the amount of dry matter produced and the amount of water transpired, expressed as the water use efficiency (Wit 1958, Dewar 1997). From a physiological and ecological point of view, these concepts are interesting because they represent a summary of forest ecosystem responses to the environment. The coefficients characterize the resource use efficiencies of different ecosystems and they can be compared easily. By using physiological knowledge about the existing links between the different processes of forest transpiration and forest growth, confidence in the simple relations can be obtained (Dewar 1997). Attempts are made to understand the physiological basis of the conservative quantities of the light use efficiency and the water use efficiency, and to theoretically predict the values of these constants (e.g., Monteith 1990, Dewar 1996, Landsberg et al. 1996).

One simple model that combines these attractive features is the Rescap model. This model of light and water use originally developed for crops (Monteith 1986, Monteith et al. 1989) was adapted and evaluated for trees in Dewar (1997). The model was validated in Dewar (1997) rather indirectly by the simulation of soil water contents, whereas the most interesting model outputs are forest growth and forest transpiration.

Our research aims at testing a slightly adapted version of the Rescap-model, in which the linear relation between intercepted radiation and forest growth was replaced by a curve-linear relation. This model was applied to half-hourly and daily carbon and water fluxes of a Douglas fir forest (*Pseudotsuga menziessii* (Mirb.) Franco) in the Netherlands. The interpretability of the model parameters was tested by parameterising the model on two years of flux data: one year before and one year after a thinning took place. The changes in light use efficiency and water use efficiency were evaluated in relation to the thinning. We also applied a sensitivity analysis to test whether the changes in parameter values were real shifts in ecosystem functioning, and the interpretability of these changes is not hampered by large parameter uncertainties. The respiration and assimilation components are evaluated by comparison to results of the process-based model FORGRO (Mohren 1987, Kramer and Mohren 1996, Van Wijk et al. 2000b).
METHOD

Site description
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 under-story in 1995. Mean tree height between 1990 and 1992 was 21.6 m. Projected leaf area index ranged from 7.8 to 10.5 m\(^2\) 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). In the winter of 1995 – 1996 a thinning took place in which about one third of the trees was cut.

The soil at Speulderbos is a Haplic Podzol, well drained, and consisting of fluviatile 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 data were collected 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) and Bosveld et al. (1998). 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 water vapour 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). Night-time 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 night-time CO\(_2\)-fluxes from the 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 used in this article was 30 minutes. Due to the influence of a neighbouring oak forest, data were removed from the data set when the wind was from the southwest. Sap flow in 1995 and 1996 was measured using the Granier method (Granier 1985). Measurements were performed on eleven trees. All sap flow data were set to zero every night, weighted to the sapwood area of the measured trees and scaled to eddy covariance measurements of water vapour, using daily total sap flow from 6 a.m. to 6 a.m. to avoid problems associated with a possible time lag.
The adapted Rescap-model (Rescap_H: half-hourly fluxes and Rescap_D: daily fluxes)
The carbon flux is divided into an assimilation-term, which we assume purely radiation driven, and a respiration term, which we assume temperature driven. The assimilation relation is given by a saturated curve-linear relation; this formulation of the relationship is chosen because the simple conceptual interpretation of the two coefficients.

\[ Ass = \frac{a \times Rg}{b + Rg} \]  

(1)

In which:
‘Rg’ 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\(^{-1}\)

The respiration relation:

\[ R = c \times 2^{\frac{T-25}{10}} \]  

(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 assimilation transpiration relation we used the Vapour Pressure Deficit [VPD] -correction as shown in the appendix of Dewar (1997):

\[ T = \frac{1}{q_o} \times Ass \times (\frac{1}{D} + \frac{1}{D_0})^{-1} \]  

(3)

In which:
‘T’ is transpiration (in mm H\(_2\)O d\(^{-1}\)), ‘q\(_o\)’ 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)

Parameterisation of Rescap
Two different model parameterisations were used: the half-hourly version of the Rescap-model [Rescap_H] was based on the half hourly data of eddy covariance carbon and water fluxes in combination with the half hourly input values of radiation, temperature and VPD. The further simplified daily version of
<table>
<thead>
<tr>
<th></th>
<th>1995</th>
<th>1996</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rescap_H CO₂</td>
<td>2093</td>
<td>3823</td>
</tr>
<tr>
<td>Rescap_H H₂O</td>
<td>1490</td>
<td>1879</td>
</tr>
<tr>
<td>Rescap_D CO₂</td>
<td>43</td>
<td>110</td>
</tr>
<tr>
<td>Rescap_D H₂O</td>
<td>60</td>
<td>247</td>
</tr>
</tbody>
</table>

Rescap [Rescap_D] was based on daily values of eddy covariance carbon fluxes, daily values of the sap flow and daily values of the input variable. Both models were parameterised on 1995 and 1996 data. As a thinning took place in the winter of 1995-1996 in which one third of the trees was cut, the models can be tested on how this thinning is represented in the optimised parameter values.

The parameters of both Rescap_H and Rescap_D were optimised with the Simplex-optimisation method (Press et al. 1989) based on measured carbon and water vapour fluxes in periods in which there was no water stress (Van Wijk et al. 2000b). The quantity of data available for the parameterisation is given in Table 1. In 1995 measured data were only available from day of year 180 onward. This resulted in fewer data available for parameterisation for 1995 than for 1996. To test whether this influenced the comparison of the optimised parameter-values, the 1996 parameters were also optimised with data from day of year 180 onward. The effects of the limited data availability of 1995 were further tested in the sensitivity analysis (See 'Evaluation of Rescap').

**Evaluation of Rescap**

Both Rescap-models were tested and evaluated by, first, a comparison of the model performances to those of the process-based FORGRO model, parameterised for Speuld for both years separately (Van Wijk et al. 2000a, Van Wijk et al. 2000b). Second, by a comparison of the estimated respiration and assimilation amounts to the amounts estimated by FORGRO. In this way the effects of the assumption that assimilation is purely driven by radiation were evaluated, and the distinction made by the Rescap-models between respiration and assimilation was tested. An extensive description of the process-based forest growth model FORGRO can be found in Kramer and Mohren (1996) and Mohren (1987). The concepts of the model are the standard leaf photosynthesis model of Farquhar et al. (1980), the stomatal conductance model of Leuning (1995), a layered radiation interception model (Goudriaan and Van Laar 1994) and respiration calculations as applied in Van Wijk et al. (2000b).

Third, changes in parameter values of the 1995-models versus the 1996 models were tested by a sensitivity analysis. In this analysis the Rescap-models were run with a Monte-Carlo simulation with 50 values of each parameter. All model parameterisations with a model outputs within two times the standard
deviations of the half-hourly fluxes for Rescap_H and within two times the standard deviations of the daily summed fluxes for Rescap_D were accepted. The daily standard deviations were calculated with:

\[ \sigma_D = \sqrt{\frac{\sum_{i=1}^{48} \sigma_H}{48}} \]

In which \( \sigma_D \) is the daily standard deviation and \( \sigma_H \) is the half-hourly standard deviation.

As the sap flow measurements were scaled on the eddy covariance measurements of water vapour, and because we want to compare the parameter sensitivity of half-hourly versus the daily model, we calculated the standard deviations of the daily transpiration from the standard deviations of the half hourly water vapour fluxes. To perform this analysis we had to define measurements outside the uncertainty intervals as outliers. About 30 half hourly measurements and two daily values were indicated as outliers.

The accepted parameter values of 1995 and 1996 were plotted in the same graphs to evaluate whether the shift in accepted parameter clusters was a clear change in ecosystem efficiency or a minor shift in an uncertain parameter space. The limited data availability of 1995 was tested by comparing the accepted 'clouds' of parameter combinations with those of 1996. If the data availability of 1995 influenced the parameter sensitivity of the daily model this would result in larger 'clouds' of accepted parameter combinations for 1995 than for 1996.

**RESULTS**

First, simulated half-hourly water and carbon fluxes of the modified Rescap model are presented. The optimised model parameters, performance and a comparison with the results of the process-based model FORGRO are shown separately for the half-hourly fluxes of 1995 and 1996, together with the results of a sensitivity analysis in which the uniqueness and thereby the potential for functional interpretation of the model parameters were assessed. In the second subsection the same results are presented for the daily carbon and water exchange values.

**Rescap_H**

The optimised values of the Rescap_H model parameters are presented in Table 2. The values showed clear differences between 1995 and 1996. The performances of the models are presented in Table 3 together with the performances of FORGRO. Plots of the model simulations versus the measured values are given in Figure 1; the fluxes of both years are plotted on the same scale. In comparison to the process-based model FORGRO, the performance of the Rescap-H models showed to be better for carbon and equally well for water.
### Table 2: Parameter values of Rescap_H for Speuld 1995 and 1996

<table>
<thead>
<tr>
<th>Coefficient</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 CO₂ m⁻² d⁻¹]</td>
<td>160.7</td>
<td>91.6</td>
</tr>
<tr>
<td>b [MJ m⁻² d⁻¹]</td>
<td>38.0</td>
<td>18.7</td>
</tr>
<tr>
<td>a / b [g CO₂ 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 CO₂ m⁻² d⁻¹]</td>
<td>41.5</td>
<td>30.2</td>
</tr>
<tr>
<td><strong>Transpiration</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>q₀ [g CO₂ kg H₂O⁻¹ kPa]</td>
<td>3.4</td>
<td>3.0</td>
</tr>
<tr>
<td>D₀ [kPa]</td>
<td>0.26</td>
<td>0.23</td>
</tr>
</tbody>
</table>

### Table 3: Performance of the Rescap_H Model on measured carbon and water vapour exchange (given are RMSE (for carbon in g CO₂ m⁻² d⁻¹ and for water in mm H₂O d⁻¹) and between brackets the explained variance) in comparison to FORGRO

<table>
<thead>
<tr>
<th></th>
<th>Performance of Rescap H</th>
<th>Performance of FORGRO</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carbon exchange 1995</td>
<td>20.0 (0.76)</td>
<td>21.2 (0.73)</td>
</tr>
<tr>
<td>Carbon exchange 1996</td>
<td>20.9 (0.58)</td>
<td>21.6 (0.56)</td>
</tr>
<tr>
<td>Water vapour fluxes 1995</td>
<td>1.00 (0.87)</td>
<td>1.02 (0.86)</td>
</tr>
<tr>
<td>Water vapour fluxes 1996</td>
<td>0.86 (0.77)</td>
<td>0.85 (0.80)</td>
</tr>
</tbody>
</table>

### Table 4: Comparison of simulated assimilation and respiration amounts for 1995 and 1996 of Rescap and FORGRO (given are values of (sum of Rescap) / (sum of FORGRO))

<table>
<thead>
<tr>
<th></th>
<th>Half-Hourly</th>
<th>Daily</th>
</tr>
</thead>
<tbody>
<tr>
<td>respiration 1995</td>
<td>0.82</td>
<td>0.97</td>
</tr>
<tr>
<td>assimilation 1995</td>
<td>0.88</td>
<td>0.99</td>
</tr>
<tr>
<td>respiration 1996</td>
<td>1.13</td>
<td>1.14</td>
</tr>
<tr>
<td>assimilation 1996</td>
<td>1.13</td>
<td>1.08</td>
</tr>
</tbody>
</table>
The separation of the carbon fluxes into an assimilation part and a respiration part was close to the simulated values of FORGRO as the explained variance of the FORGRO simulated respiration by the Rescap_H respiration was 0.98, with no significant deviation from the 1:1 relation (results not shown). The response used in Rescap_H is therefore a good summary of all the respiration responses of the different forest compartments to temperature in FORGRO, like the canopy, tree bole and soil. In Table 4 the simulated totals of respiration and assimilation of the Rescap_H models are compared with the values estimated by FORGRO. The results showed that the estimation of the Rescap_H models was close to the FORGRO-values and that thereby the division of the total CO₂-flux into a respiration and assimilation component by the Rescap-model can be considered to be reliable.

Figure 2 shows the results of the sensitivity analysis of the 1995 and 1996 models. The accepted values of the different parameters were clearly correlated with each other. In the case of the 'q₀' and the 'D₀'-parameters the clusters of the accepted parameter values of 1995 and 1996 could not be distinguished. The difference in the optimised values of these parameters as presented in Table 2 was therefore not significant.
In the carbon part of Rescap_H the change in the 'a' (the light saturated assimilation) and 'c'-coefficients (respiration coefficient) was clear, whereas the 'a/b'-coefficient (initial light use efficiency) did not change significantly.

**Rescap_D**

The optimised parameter values of Rescap_D are presented in Table 5 and the performance is presented in Table 6, and in Figure 3 and 4; also here the y-axes are the same for both years. The performance of the Rescap_D model in simulating measured daily water-fluxes was similar to the FORGRO-performance. However, the performance in simulating measured daily carbon-fluxes was clearly lower than the FORGO-model, both expressed in $R^2$ as in RMSE.

In Figure 5 the accepted parameter combinations of Rescap_D are presented in a similar way as for the Rescap_H model. The shifts in parameter values differed from the Rescap_H model. The Rescap_D model showed significant shifts in the 'q_0', 'D_0' and 'a/b'-coefficients, whereas the shifts in the 'a' and 'c'-coefficients were only minor compared to the large intervals of accepted parameter-values. The accepted parameter 'clouds' of Rescap_D were larger than the parameter 'clouds' of Rescap_H: this indicated lower parameter-
Table 5: Parameter values of the Rescap_D for Speuld 1995 and 1996

<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$_2$ m$^{-2}$ d$^{-1}$]</td>
<td>45.2</td>
<td>50.6</td>
</tr>
<tr>
<td>$b$ [MJ m$^{-2}$ d$^{-1}$]</td>
<td>11.3</td>
<td>20.5</td>
</tr>
<tr>
<td>$a/b$ [g CO$_2$ MJ$^{-1}$]</td>
<td>4.0</td>
<td>2.5</td>
</tr>
<tr>
<td><strong>Respiration</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$c$ [g CO$_2$ m$^{-2}$ d$^{-1}$]</td>
<td>25.9</td>
<td>19.8</td>
</tr>
<tr>
<td><strong>Transpiration</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$q_0$ [g CO$_2$ kg H$_2$O$^{-1}$ kPa]</td>
<td>3.6</td>
<td>2.0</td>
</tr>
<tr>
<td>$D_0$ [kPa]</td>
<td>0.5</td>
<td>0.14</td>
</tr>
</tbody>
</table>

Sensitivity for Rescap_D than for Rescap_H. The size of the accepted parameter clouds of 1995 and 1996 showed no clear differences in size for the carbon part of Rescap_D. The size of the 1995 parameter cloud of the water part of the model (consisting of accepted $q_0$ and $D_0$ values) did not influence whether the change in these coefficients was considered significant or not.

A parameter optimisation was also performed using only 1996 data from day of year 180 onward, the same period as data were available in 1995. The optimised parameters were close to the optimised for the total year: $a$ - coefficient was 52.3 g CO$_2$ m$^{-2}$ d$^{-1}$, $b$ was 22.3 MJ m$^{-2}$ d$^{-1}$, $c$ was 23.7 g CO$_2$ m$^{-2}$ d$^{-1}$, $q_0$ was 2.6 g CO$_2$ kg H$_2$O$^{-1}$ kPa and $D_0$ was 0.19 kPa. These values are within the uncertainty ‘clouds’ of the different coefficients (see Figure 5).

In Table 4 the division into respiration and assimilation components is evaluated by the summed totals. The day-to-day variations were very close to the FORGRO simulation results. In the summed totals the relative values of 1995 are very close to one, whereas the 1996 values showed a larger deviation from the ideal value of one.
Table 6: Performance of the Rescap_D on FORGRO and daily measured carbon exchange and forest transpiration (given are RMSE and between brackets the explained variance)

<table>
<thead>
<tr>
<th></th>
<th>Rescap_D</th>
<th>FORGRO</th>
</tr>
</thead>
<tbody>
<tr>
<td>Measured carbon exchange 1995</td>
<td>66.2 (0.43)</td>
<td>49.1 (0.55)</td>
</tr>
<tr>
<td>Measured carbon exchange 1996</td>
<td>53.3 (0.46)</td>
<td>48.1 (0.58)</td>
</tr>
<tr>
<td>Measured transpiration 1995</td>
<td>0.30 (0.91)</td>
<td>0.27 (0.92)</td>
</tr>
<tr>
<td>Measured transpiration 1996</td>
<td>0.22 (0.84)</td>
<td>0.27 (0.80)</td>
</tr>
</tbody>
</table>

Figure 3: Measured and simulated daily carbon and transpiration fluxes for Speuld 1995
DISCUSSION

The performance of both Rescap_H and Rescap_D was satisfactory. The performance in simulating the water fluxes was similar to or sometimes even slightly better than the process-based model FORGRO. The half hourly carbon fluxes were simulated better by Rescap_H than by FORGRO, whereas the daily carbon exchange was simulated less well by Rescap_D than by FORGRO. The relatively lower performance of Rescap_D is probably caused by the aggregation of half-hourly temperature and radiation values into one mean or total daily value, which is used as an input for Rescap_D. In this aggregation information is lost, for example about non-linearity, which resulted in a lower performance.

The differences in the optimised coefficients of Rescap_H and Rescap_D for 1995 and 1996 show interesting features. Whereas Rescap_H showed significant changes in the 'a' and 'c' coefficients (saturated assimilation and respiration) Rescap_D showed significant changes in the 'q_0', 'D_0' and 'a/b'-coefficients (respectively the water use efficiency, the VPD-sensitivity and the initial light use efficiency). The shifts in the Rescap_H coefficients show that the coefficients of this model can be interpreted in terms of tree physiological characteristics and stand characteristics. The coefficients that did not change, 'q_0', 'D_0' and 'a/b', can
be considered as more physiologically determined by their definition. The efficiency of assimilation versus water use and the 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. Both the saturated assimilation and the respiration coefficient are much 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, Rescap_H should be tested on other forests to determine whether the linkage between Leaf Area Index and the model parameters is generally applicable.

The separation into physiologically linked and stand characteristicallinked coefficients is not clear with Rescap_D. With this model the sequence of changing and non-changing coefficients is exactly opposite to Rescap_H. Two factors probably cause this difference. First, the non-linear aggregation effect of the temperature and radiation inputs versus the daily summed values of transpiration and carbon exchange outputs. This aggregation leads to a shift in the

Figure 5: Accepted parameter values of the daily models of 1995 and 1996 (for explanation see text); the coefficient not shown in the diagrams of the carbon part of the model is at its optimal value, see Table 5.
depths of concavity in the equations (Rastetter et al. 1992) and thereby to shifts in the functional interpretability of the parameters. Another effect is a decreased parameter sensitivity as is shown in Figure 5 compared to Figure 2. By aggregation the relative ranges of the radiation and temperature inputs decrease, for example the half-hourly global radiation varies from 0 to 900 Wm\(^{-2}\) where the daily global radiation varies from 1 to 30 MJ m\(^{-2}\) d\(^{-1}\). This decrease in relative range of the input variables will lead to a decrease in parameter sensitivity.

The difference between parameter shifts between 1995 and 1996 is a clear disadvantage of the daily version. Where Rescap_H shows potentials for linking stand characteristics to the 'a' and 'c' coefficients and linking 'q_0', 'D_0' and 'a/b' to physiological characteristics of species, this is not the case for Rescap_D. In this study the parameters of Rescap_D are just fit parameters without a clear functional interpretation, due to the aggregation effects that are incorporated into the parameter values. This limits the application possibilities for Rescap_D.

An important question in this comparison is whether the results were influenced by the limited period of data-availability in 1995. This could have two effects: first, it can influence the optimised values of the different coefficients. However, as the parameter optimisation of a limited period of 1996 data (from day of year 180) showed similar parameter values as for the total set of 1996 data, this problem did not seem to have biased our results. Second, the limited data availability can decrease the parameter sensitivity. The results of the sensitivity analysis shown in Figure 5 did not indicate this effect except for the water part of Rescap_D. However, the significance of the changes in the 'q_0' and 'D_0'-coefficients from 1995 to 1996 was not determined by the data availability.

Another important factor for the comparison of parameter values is the reliability of the division of the carbon flux into an assimilation and respiration component. The best estimate we had of such a division was the outcome of the process-based model FORGRO. By considering the results of this model as 'truth', we tried to gain confidence in the derived coefficients. In this case the estimates of respiration and assimilation of the Rescap-models and of FORGRO were in reasonable agreement, using the optimised parameter values. Both the half-hourly and the daily model overestimated the respiration of 1996, compared to FORGRO. Maybe this is caused by the increased inhomogeneity in the forest, due to the thinning: radiation was not that determining as in the 1995 case. However, the broad range of accepted parameter combinations, especially for the Rescap_D model, indicate that the separation into assimilation and respiration is rather uncertain. As a consequence of the correlated input values of temperature and radiation an increase in the respiration coefficient can be compensated by the model with an increased saturated assimilation coefficient, with only a limited decrease in model performance. Due to the difficulties in measuring CO_2-fluxes at night, this problem could not be solved by dividing the data set into a respiration-subset consisting of only nightly respiration CO_2-fluxes and a high radiation subset to calculate the saturated assimilation. The large errors in the night-time fluxes result in a large error in the estimated respiration coefficient, and thereby also in larger errors in the other coefficients.
The sensitivity analysis for both Rescap_H and Rescap_D showed that strong correlations exist between the accepted parameter-values. This is a consequence of correlations between input variables (for example temperature and radiation) and the chosen model (for example, the 'a'-coefficient is present both as the saturated assimilation and as a factor in the initial light use efficiency, 'a/b'). If the goal of the application of these simple models is to derive parameters that quantify ecosystem functioning, such an analysis is crucial for comparison of the derived values. A presentation of only the optimised values of the parameters as has been done until now (Baldocchi et al. 1987, Dewar 1997) can give strong biased results.

For a broad application of these kind of simple models it will be essential to relate the parameters of the model to ecosystem characteristics that are (relatively) easy to measure, like the leaf area index. A combination of model research and field research will be necessary for this. An advantage of relating these ‘functional interpretable’ coefficients to forest characteristics, is an open model structure: the model rules will be easy to interpret and model-communication will be improved.

REFERENCES


