Modeling stomatal conductance is a key element in predicting tree growth and water use at the stand scale. We compared three commonly used models of stomatal conductance, the Jarvis-Loustau, Ball-Berry and Leuning models, for their suitability for incorporating soil water stress into their formulation, and for their performance in modeling forest ecosystem fluxes. We optimized the parameters of each of the three models with sap flow and soil water content data. The optimized Ball-Berry model showed clear relationships with air temperature and soil water content, whereas the optimized Leuning and Jarvis-Loustau models only showed a relationship with soil water content. We conclude that use of relative humidity instead of vapor pressure deficit, as in the Ball-Berry model, is not suitable for modeling daily gas exchange in Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) in the Speulderbos forest near the village of Garderen, The Netherlands. Based on the calculated responses to soil water content, we linked a model of forest growth, FORGRO, with a model of soil water, SWIF, to obtain a forest water-balance model that satisfactorily simulated carbon and water (transpiration) fluxes and soil water contents in the Douglas-fir forest for 1995.

Keywords: carbon fluxes, Pseudotsuga menziesii, simulation models, soil water content, transpiration.

Introduction

Process-based forest models are essential for understanding and predicting tree growth and water use on a stand scale, and for assessing possible effects of climate change (Houghton et al. 1990). The underlying processes of CO₂ exchange between the atmosphere and individual leaves are relatively well understood (Dewar 1997). There is also general consensus about the use of the Farquhar approach (Farquhar et al. 1980) for modeling leaf photosynthesis. Furthermore, carbon exchange at the leaf level can be scaled up to the canopy level by using models for radiation interception (e.g., Wang and Jarvis 1990, Falge et al. 1996, Williams et al. 1997).

A key element in modeling fluxes in forest ecosystems for which no clear consensus exists is stomatal conductance (Monteith 1995). There are two main approaches to modeling stomatal conductance. The purely empirical approach makes use of a set of response functions to link stomatal conductance through fitted response functions to environmental variables (Jarvis 1976, Stewart 1988). A wide range of model types and variables is currently used, indicating an incomplete knowledge of relationships between stomatal conductance and environmental variables and a failure to represent plant physiological parameters accurately. In all of these models, the calibrated values of parameters change if another response is added (Lankreijer 1998).

The second approach is through physiologically oriented models in which stomatal conductance is linked directly and indirectly through photosynthesis to the environment (Lankreijer 1998). Several of these models link stomatal conductance to leaf water potential (Whitehead and Hinckley 1991), whereas other models link stomatal conductance directly to photosynthesis. Stomatal conductance models based on leaf water potentials are not discussed in this article.

Leaf-scale stomatal conductance models based on a direct link between photosynthesis and stomatal conductance are widely used because they require the linking of only a few empirical parameters to plant-specific characteristics, and are easy to incorporate into growth and ecosystem models (Tenhunen et al. 1990, Leuning 1995). Two common models of this type are the Ball-Berry model (Ball et al. 1987) and the Leuning model (Leuning 1995). The Ball-Berry model uses net assimilation, CO₂ concentration in the leaf boundary layer and relative humidity in the leaf boundary layer (Ball et al. 1987). Because the use of relative humidity is questionable (Aphalo and Jarvis 1993, Monteith 1995), Leuning adapted the Ball-Berry model by substituting vapor pressure deficit at the leaf surface for relative humidity (Leuning 1995).
Although the effects of soil drought on stomatal conductance have been demonstrated in many field and laboratory experiments (Baldocchi 1997), the Ball-Berry and Leuning models do not specifically incorporate a water stress function. In both models, it is assumed that the empirical constant $g_{\text{fac}}$, which couples stomatal conductance to the empirical relationship between assimilation, humidity (deficit) and the CO$_2$ concentration at the boundary layer, can be related to soil water content to account for water stress effects (Tenhunen et al. 1990). However, no clear relationship between $g_{\text{fac}}$ and soil water content has been demonstrated, although $g_{\text{fac}}$ is related to other properties characterizing water status, such as needle water potential (Sala and Tenhunen 1996). In contrast to the Ball-Berry and Leuning stomatal conductance models, the Jarvis-Stewart-like models incorporate a specific soil water stress function by including a response function to soil water deficit (Jarvis 1976, Stewart 1988).

We compared the Ball-Berry model, the Leuning model, and a modified Jarvis-Stewart-like model, the Jarvis-Loustau model (Granier and Loustau 1994, Loustau et al. 1997) to determine if soil water stress could be incorporated in their formulation. Soil water stress was incorporated by relating stomatal conductance to soil water content. We also determined their performance in simulating daily transpiration fluxes of a Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) forest by linking them with the forest growth model FORGRO (Mohren 1987, Kramer 1996) and the forest soil water model SWIF (Tiktak and Bouten 1992) to produce a forest water-balance model. All three stomatal conductance models were included into the same forest water-balance model. The models were parameterized with transpiration data obtained in 1989 for Douglas-fir at the Speulderbos forest. For the two stomatal conductance models that were modified to incorporate a soil water stress function, fluxes of transpiration and carbon, as well as soil water content for 1995, were simulated to test the models.

Materials and methods

Site description

Data were obtained from a 2.5-ha Douglas-fir stand within a large forested area (Speulderbos) near the village of Garderen, The Netherlands. The stand, which was planted in 1962, had a stocking density of 780 trees ha$^{-1}$ and had no understory. Mean tree height between 1990 and 1992 was 21.6 m. Projected leaf area index ranged from 7.8 to 10.5, according to estimates made by sampling needles at different heights in different trees, and multiplying the measured leaf densities by the tree density (Jans et al. 1994). The soil at Speulderbos is a well-drained Haplic Podzol, consisting of fluviatile deposits with textures ranging from fine sand to sandy loam. The water table is at 40 m. The 30-year, mean annual rainfall is 834 mm.

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Simulation models

Soil water content was calculated with the SWIF model, which describes vertical water flow and root water uptake in the unsaturated soil zone. The model also incorporates soil evaporation as formulated by Schaap and Bouten (1997) and distributes root water uptake over several soil layers based on relative root density per layer (Tiktak and Bouten 1992). The SWIF inputs are precipitation and the soil physical characteristics that are expressed with the Van Genuchten equations.

Meteorological data were collected by the Royal Meteorological Institute of The Netherlands (KNMI) from a 36-m tower (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 water vapor and CO$_2$ (Kohsiek 1991), mounted 30 m above the forest floor. Carbon dioxide concentrations were measured at heights of 24 and 36 m with an LI-6262 infrared gas analyzer (IRGA) (Li-Cor, Inc., Lincoln, NE). 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 the CO$_2$ concentration profiles. The CO$_2$ 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 min. Because of the influence of a neighboring oak forest, data were omitted from the analysis when the wind was from the southwest.

In 1989, sap flow was measured by the calibrated heat pulse velocity method (HPV) (Marshal 1985) on seven trees to estimate tree transpiration without soil evaporation (Bouten 1992). In 1995, sap flow was measured by the Granier method (Granier 1985), with one sensor per tree, on six trees located near the tower. All sap flow data were set to zero each night. The data were weighted according to the sapwood area of the measured trees (ranging from 1.1 to 3.7 dm$^2$) and scaled to eddy covariance measurements of water vapor based on daily total sap flow from 0600 to 1500 h to avoid problems associated with a possible time lag. Differences between the two sap flow measurement techniques were ignored because the results of both methods were scaled to eddy covariance measurements of latent heat fluxes.

During 1989, soil water was measured weekly by time domain reflectometry (TDR) and a neutron-scattering method. The TDR probes were placed between trees for which sap flow was being measured. Data from the forest soil water model SWIF (Soil Water in Forested Ecosystems), calibrated on this forest site (Bouten et al. 1992), were used to interpolate these measurements. In 1995, soil water was measured two to four times each day with an automated TDR system consisting of 18 probes (Heimovaara and Bouten 1990). The values of the various probes were averaged to obtain a mean daily soil water content of the upper 50 cm of soil.
Carbon and transpiration fluxes of the forest were calculated with the process-based forest growth model FORGRO. Inputs are radiation, air temperature, wind speed, early-morning vapor pressure and precipitation. Outputs of FORGRO may vary from daily transpiration and carbon exchange to yearly forest yield. Central to FORGRO is the description of the attenuation of radiance in a canopy whose homogeneity 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 photosynthetically active radiation (PAR), near infrared radiation (NIR), daily gross photosynthesis and transpiration are calculated by integrating hourly over both sunlit and shaded leaf layers with a Gaussian integration scheme (Goudriaan and Van Laar 1994).

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 is related to temperature by the Arrhenius approach, whereas growth respiration is assumed to be insensitive to changes in temperature (Goudriaan and Van Laar 1994).

To calculate daily carbon exchange, soil respiration rates (\( S_{\text{resp}} \)) were calculated with a model based on the concept of multiplicative interaction (Freijer et al. 1996, Stroo et al. 1989):

\[
S_{\text{resp}} = S_i \left( \frac{\exp(-k_i(T - T_{\text{opt}})^2)}{\exp(-k_i(T_i - T_{\text{opt}})^2)} \right) \theta_i\theta_{\text{e}},
\]

where \( T \) is temperature (°C), \( \theta \) is soil water content (m\(^3\) m\(^{-3}\)), \( S_i \) (kg CO\(_2\) ha\(^{-1}\) day\(^{-1}\)) and \( \theta_i \) (m\(^3\) m\(^{-3}\)) are empirical coefficients, \( \theta_{\text{e}} \) (m\(^3\) m\(^{-3}\)) and \( \theta_i \) (m\(^3\) m\(^{-3}\)) are empirical coefficients, \( \theta_{\text{e}} \leq 1.5, T_i = 20 \, ^\circ\text{C}, T_{\text{opt}} = 46.2 \, ^\circ\text{C}, \) and \( k_i = 1.902 \pm 10^{-3} \, ^\circ\text{C}^{-1} \) (Freijer et al. 1996).

The model of leaf photosynthesis (Falge et al. 1996) used in this version of FORGRO is based on the approach of Farquhar et al. (1980) and the model formulation of Harley and Tenhunen (1991). This photosynthesis model was used to calculate photosynthesis, transpiration and stomatal conductance within each leaf layer. Leaf photosynthesis parameters were obtained from leaf chamber measurements. To calculate leaf photosynthesis and transpiration, we assumed that there were no gradients of CO\(_2\), water vapor or temperature within the canopy. Air temperature and humidity measured in the tower at 18 and 30 m showed no large systematic differences.

We incorporated three models of stomatal conductance \( (G_s) \) into the model of leaf photosynthesis (without a function for soil water stress). The Ball-Berry model (Ball et al. 1987) was incorporated as:

\[
G_s = \frac{g_{\text{BB}}}{C_s}, \quad (2)
\]

where \( g_{\text{BB}} \) is an empirical coefficient, \( A \) is net assimilation (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)), \( R_i \) is relative humidity, and \( C_s \) is the boundary layer CO\(_2\) concentration (\( \mu \text{l} \text{l}^{-1} \)).

The Leuning model (Leuning 1995) was incorporated as:

\[
G_s = \frac{A}{(C_s - \tau)(1 + D/D_0)}, \quad (3)
\]

where \( g_{\text{TL}} \) and \( D_0 \) (kPa) are empirical coefficients, \( \tau \) is the CO\(_2\) compensation point (\( \mu \text{l} \text{l}^{-1} \)), and \( D \) is vapor pressure deficit (kPa).

The Jarvis-Loustau model (Loustau et al. 1997) was incorporated as:

\[
G_s = \frac{R_i}{k_1 + R_s} \left( 1 - k_s \delta q \right), \quad (4)
\]

where \( g_{\text{max}} \) (m \text{s}^{-1}), \( k_1 \) (W m\(^{-2}\)), \( k_2 \) (kPa\(^{-1}\)) and \( k_3 \) (kPa\(^{-1}\)) are empirical coefficients, \( R_i \) is global radiation (W m\(^{-2}\)) and \( \delta q \) is specific humidity deficit (kPa).

Leaf assimilation, transpiration and stomatal conductance were calculated for the Ball-Berry and Leuning models based on the coupled photosynthesis–conductance model presented by Leuning (1990). For the Jarvis-Loustau model, stomatal conductance was calculated with the values of the driving variables of the model, after which leaf photosynthesis and transpiration were calculated analytically. Leaf transpiration was calculated using the simulated gradient of water vapor inside the leaf (set at a relative humidity of 1) and the leaf boundary layer. Boundary layer conductance was calculated according to Nobel (1983) and modified for conifers as suggested by Jarvis et al. (1976).

Model parameterization

The empirical coefficients for the three stomatal conductance models were determined from the 1989 sap flow data. This was done by minimizing the difference expressed in normalized root mean square error (NRMSE) between daily measured transpiration and daily simulated transpiration from Day 145 until Day 265 of 1989. The simplex method was used for the optimization (Press et al. 1989).

To incorporate any effects of soil water stress, the empirical coefficients (Ball-Berry’s \( g_{\text{BB}} \), Leuning’s \( g_{\text{TL}} \) and Jarvis-Loustau’s \( g_{\text{max}} \)) were optimized each day by minimizing the difference between modeled and measured transpiration flux. The optimized coefficients were related to soil water content data and to meteorological driving variables to obtain information about missing responses. Stomatal response to soil water content was modeled by multiplying each of Equations 2, 3 and 4 by the standard response function used by Jarvis (1976) and Stewart (1988):

\[
f_i = 1 - k_i \exp(k_x S), \quad 0 \leq S \leq 1 \quad (5)
\]

\[
f_i = 1 - k_i \quad S < 0, \quad (6)
\]
where

$$S = \frac{\theta_r - \theta}{\theta_t - \theta_w} \quad (7)$$

and \(\theta_t\) and \(\theta_w\) are the volumetric soil water contents (m\(^3\) m\(^{-3}\)) at field capacity and wilting point, respectively.

We used the derived stomatal response to soil water stress to link the forest growth model FORGRO with the soil water model SWIF at each day step to create a forest water-balance model. The SWIF model calculated soil water content each day from measured rainfall minus interception (in the Speulderbos up to 50% (Bouten et al. 1992)), drainage of water, and forest transpiration calculated by FORGRO. Based on the calculated soil water content of the upper 50 cm, the Ball-Berry, Leuning and Jarvis-Loustau coefficients were updated according to the responses found with the 1989 data.

We used the linked FORGRO–SWIF model to simulate daily carbon exchange and sap flow for 1995. The validation of simulated forest transpiration was, therefore, completely independent. The model of soil respiration (\(S_{\text{resp}}\)) was parameterized by calibrating \(S_r\) and \(\theta_r\) against the difference between daily modeled CO\(_2\) fluxes without the root and soil respiration calculation of Equation 1 and daily measured CO\(_2\) fluxes of 1995. Values obtained were \(S_r = 71.7\) kg CO\(_2\) ha\(^{-1}\) day\(^{-1}\) and \(\theta_r = 0.11\) m\(^3\) m\(^{-3}\). Modeled rates of soil respiration varied in summer from 70 to 90 kg CO\(_2\) ha\(^{-1}\) day\(^{-1}\), which agreed well with measured values of 60–80 kg CO\(_2\) ha\(^{-1}\) day\(^{-1}\) in 1994 (unpublished measurements by A. Tietema, University van Amsterdam).

The leaf area index used in the model was less than that measured in spring (7.8) or in summer (10.5). These higher values reflect the presence of senescent needles in the lower leaf layers. Leaf chamber measurements showed hardly any respiration or assimilation fluxes in the lower layer of the canopy. To account for the effects of decreasing respiration and assimilation activity of the needles in the lower canopy, it is common to introduce a vertical gradient of nitrogen within the canopy and make leaf photosynthetic and respiration parameters dependent on leaf nitrogen concentration (Friend 1991, Kull and Jarvis 1995). However, because we did not determine the relationships between leaf N and the photosynthetic and respiration coefficients, we chose another approach for modeling daily carbon fluxes. Net assimilation was optimized during the growing season so that only needles with a positive carbon gain were included (cf. Hauhs et al. 1995). Such optimization gave an LAI value of 7.0, which was incorporated into the model as a first approximation.

### Results and discussion

The modeling results are presented and discussed in four stages, because the results of each stage depend on the results of the previous stage. In Stage 1, the three stomatal conductance models were optimized without water stress. In Stage 2, the data were examined daily to identify systematic errors in the models that were related to soil water content and air temperature. In Stage 3, we coupled the models FORGRO and SWIF to each of the stomatal conductance models that could include soil water stress, to obtain a forest water-balance model. In Stage 4, we simulated transpiration, carbon exchange and soil water contents for 1995.

### General optimization of parameters

Parameters for the three models of stomatal conductance without functions for soil water stress are given in Table 1, together with model fit values to the 1989 transpiration data. The Jarvis-Loustau model performed better than the Ball-Berry model, as was expected because the Jarvis-Loustau model has four fitted parameters, whereas the Ball-Berry model has only one fitted parameter. The model parameters presented here are not the leaf physiological parameters of Douglas-fir. Because they were derived by an inverse modeling method in which a large amount of scaling was involved, the derived parameters are model specific, or more precisely, FORGRO-dependent.

### Optimizing daily performance

With the parameters obtained from this general optimization, coefficients \(g_{\text{f-L}}\) (Leuning), \(g_{\text{f-BB}}\) (Ball-Berry) and \(g_{\text{max}}\) (Jarvis-Loustau) were optimized with day-to-day data. Because the three models were scaled up in the same way, day-to-day variation in model parameters could be compared.

Optimized values of \(g_{\text{f-L}}\), \(g_{\text{f-BB}}\), and \(g_{\text{max}}\) were plotted against daily values of soil water content and daily mean temperature (Figure 1). Although scatter was large, the effects of the different variables were evident. The large scatter is not surprising, because both model and measurement errors were incorporated into the optimized parameters.

Of the three models, the Jarvis-Loustau model showed the clearest effect of soil water content on optimized \(g_{\text{max}}\) values. Probably because of the large number of parameters, the effects of the different physical driving variables such as radiation and temperature could be distinguished clearly from the effect of soil water stress.

Of the two models with a low number of fitted parameters, optimized \(g_{\text{f-BB}}\) was related to both soil water content and daily mean temperature, whereas \(g_{\text{f-L}}\) showed a relationship only with water content. These results support the suggestion of

Table 1. Comparison of optimization of the three stomatal conductance models with daily transpiration data of 1989.

<table>
<thead>
<tr>
<th>Model</th>
<th>Ball-Berry</th>
<th>Leuning</th>
<th>Jarvis-Loustau</th>
</tr>
</thead>
<tbody>
<tr>
<td>Optimized parameters</td>
<td>(g_{\text{f-BB}} = 770)</td>
<td>(g_{\text{f-L}} = 1657)</td>
<td>(g_{\text{max}} = 0.052) m s(^{-1})</td>
</tr>
<tr>
<td>(D_0)</td>
<td>2.74 kPa</td>
<td>3.21 kPa</td>
<td>(k_1 = 132.2) W m(^{-2})</td>
</tr>
<tr>
<td>(k_2)</td>
<td>(-0.0044) kPa(^{-1})</td>
<td>(k_3 = 1.5) kPa(^{-1})</td>
<td></td>
</tr>
</tbody>
</table>

Model fit:

\(R^2\) | 0.71 | 0.75 | 0.78 |
SSE   | 38.6 mm\(^2\) day\(^{-2}\) | 29.4 mm\(^2\) day\(^{-2}\) | 25.9 mm\(^2\) day\(^{-2}\) |
NRMSE | 0.27 | 0.23 | 0.22 |
Aphalo and Jarvis (1993) that the Ball-Berry model lacks a temperature response. The difference in temperature sensitivity between the Leuning model and the Ball-Berry model cannot be explained by the extra parameter that is included in the Leuning model. The $D_0$ parameter is only a scaling coefficient to quantify the sensitivity of stomatal conductance to vapor pressure deficit. Different values of this parameter are compensated for by different values of $g_{f-L}$ and the sensitivity of the model to variations in values of $D_0$ was low. Because the Leuning model showed no relationship with temperature and differs from the Ball-Berry model in the substitution of vapor pressure deficit for relative humidity, we conclude that replacing the term for relative humidity by one for vapor pressure deficit automatically includes the temperature response for Douglas-fir, which the Ball-Berry model lacks.

Formulating the forest water-balance model

Because the Ball-Berry model showed no clear relation to soil water stress and the use of relative humidity was not valid for Speulderbos, this model was not used to formulate a forest water-balance model. One could fit a temperature and soil water content relationship based on the results of Figure 1, but this would introduce a set of new parameters and would be a difficult way of deriving the Leuning model of stomatal conductance. Water-balance models incorporating Leuning and Jarvis-Loustau models of stomatal conductance were formulated by fitting the responses of $g_{f-L}$ and $g_{max}$ to soil water content with the response function described earlier. The calculated fit responses are shown in Figure 2 with the optimized parameters.

Simulating water and carbon fluxes

Table 2 shows simulations of transpiration fluxes of 1989 and carbon exchange and transpiration fluxes of 1995 with these optimizations of the two stomatal conductance models. The

<table>
<thead>
<tr>
<th></th>
<th>Leuning</th>
<th>Jarvis-Loustau</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transpiration</td>
<td>0.97</td>
<td>0.96</td>
</tr>
<tr>
<td>Assimilation</td>
<td>1.02</td>
<td>1.05</td>
</tr>
<tr>
<td>Transpiration</td>
<td>1.09</td>
<td>1.10</td>
</tr>
</tbody>
</table>

Table 2. Comparison of simulations of daily carbon exchange and transpiration with the Leuning and Jarvis-Loustau models of stomatal conductance expressed as a ratio of the sum of simulated and measured fluxes over the measurement period, together with the explained variance, $R^2$. |
models performed similarly in explained variances, though the Leuning model gave slightly lower summations of daily calculated carbon exchange than the summations of daily calculated carbon exchange given by the Jarvis-Loustau model.

The day-to-day results of 1989 for FORGRO–SWIF with the Leuning conductance model are shown in Figure 2, both with and without a soil water stress function. Because the Jarvis-Loustau model was optimized with the same data as the Leuning model, and the same model of leaf photosynthesis and transpiration was used, day-to-day variations in the Jarvis-Loustau model and Leuning model were similar. The model variant without a water stress function overestimated transpiration around Day 220 (mid-August). The model variant containing a soil water stress function gave higher transpiration rates around Days 160 and 180 than the model variant without a water stress function. This discrepancy arises because the model variant without a water stress function had to fit transpiration rates in the period of water stress (around Day 220) as well as those in the periods in which there was no stress. The parameter values of this model variant, therefore, represent an average response to periods when soil water content was adequate and to periods when it was inadequate, whereas the model variant with the soil water stress function can distinguish between these periods, and, therefore, estimated transpiration rates more accurately during periods of water stress.

Measured and simulated carbon and transpiration fluxes for 1995 are shown in Figure 3. Figure 4 shows measured and simulated soil water contents of the upper 50 cm of 1995. Both were simulated with the Leuning model of stomatal conductance. Transpiration in 1995 was simulated satisfactorily, although the Leuning model gave slightly lower summations of daily calculated carbon exchange than the summations of daily calculated carbon exchange given by the Jarvis-Loustau model.

Figure 2. Transpiration in 1989 modeled by FORGRO–SWIF linked through the Leuning model

Figure 3. Transpiration and carbon exchange in 1995 modeled by FORGRO–SWIF linked through the Leuning model of stomatal conductance.
the simulation results of net carbon exchange of Speulderbos could not be used for independent validation of the model, but only as a qualitative test. Carbon dioxide exchange above the canopy showed a larger scatter than transpiration fluxes, which is to be expected because the uncertainty in measured CO2 exchange is greater than the uncertainty in measured sap flow. More processes contribute to the net carbon exchange of a forest than to tree transpiration, all with their own driving variables and spatial scale (e.g., growth respiration, maintenance respiration, root respiration and litter decomposition). The independent method of optimizing LAI worked well because there was no major under- or overestimation of the daily summations (see Table 2). The FORGRO–SWIF model approximated both daily flux and totals of carbon exchange, despite the many simplifying assumptions (uniform canopy, constant LAI in 1995, one air temperature and one value of soil water content used to model soil respiration).

Conclusions

The Ball-Berry model of stomatal conductance based on relative humidity is not valid for Douglas-fir in the Speulderbos. Our simulations indicate that the relative humidity term should be replaced by a term for vapor pressure deficit, as is done in Leuning’s model. Daily optimized parameters of both the Jarvis-Loustau and the Leuning models were clearly influenced by soil water content, whereas the empirical Ball-Berry parameter $g_{BB}$ depended on both soil water content and air temperature. Measured transpiration data of 1989 and 1995 were simulated satisfactorily ($R^2 = 0.81$ for 1989 and 0.88 for 1995) when a function for soil water stress was used to create the forest water-balance model FORGRO–SWIF. Predictions for daily exchange of carbon were poorer than predictions for transpiration ($R^2 = 0.55$), although there was no systematic mismatch and summations of daily carbon exchange were estimated satisfactorily. Simulated soil water content did not deviate under conditions of drought, but increments in measured soil water content caused by rainfall were underestimated.

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References


Figure 4. Measured and simulated soil water contents of the upper 50 cm of soil in 1995. Simulated values were obtained with the Leuning model of stomatal conductance.


