A comparative analysis of simulated and observed photosynthetic CO₂ uptake in two coniferous forest canopies

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Summary  Gross canopy photosynthesis ($P_g$) can be simulated with canopy models or retrieved from turbulent carbon dioxide (CO₂) flux measurements above the forest canopy. We compare the two estimates and illustrate our findings with two case studies. We used the three-dimensional canopy model MAESTRA to simulate $P_g$ of two spruce forests differing in age and structure. Model parameter acquisition and model sensitivity to selected model parameters are described, and modeled results are compared with independent flux estimates. Despite higher photon fluxes at the site, an older German Norway spruce ($Picea abies$ L. (Karst.)) canopy took up 25% less CO₂ from the atmosphere than a young Scottish Sitka spruce ($Picea sitchensis$ (Bong.) Carr.) plantation. The average magnitudes of $P_g$ and the differences between the two canopies were satisfactorily represented by the model. The main reasons for the different uptake rates were a slightly smaller quantum yield and lower absorptance of the Norway spruce stand because of a more clumped canopy structure. The model did not represent the scatter in the turbulent CO₂ flux densities, which was of the same order of magnitude as the non-photo-synthetically-active-radiation-induced biophysical variability in the simulated $P_g$. Analysis of residuals identified only small systematic differences between the modeled flux estimates and turbulent flux measurements at high vapor pressure saturation deficits. The merits and limitations of comparative analysis for quality evaluation of both methods are discussed. From this analysis, we recommend use of both parameter sets and model structure as a basis for future applications and model development.

Keywords: canopy photosynthesis model, carbon dioxide fluxes, eddy correlation, MAESTRA, Picea abies, Picea sitchensis.
carbon dioxide (CO₂) fluxes between forests and the atmosphere continuously, has made it possible to monitor the physiological functioning of a forest ecosystem as a whole and to compare the projections of process-based bottom-up models with independent flux measurements at comparable temporal resolution. However, two properties of turbulent flux observations made above the canopy restrict their use as test data for model evaluation. First, in certain meteorological conditions they may not well represent the actual ecosystem fluxes and second, the flux measured above the canopy (Fc) is the net sum of the two opposed processes, gross photosynthesis (Pg) and ecosystem respiration (Re) (Ruimy et al. 1995). Thus, Fc cannot be directly compared with the simulated gross rates. As in modeling, measured flux data are prone to errors and require thorough post-processing and quality evaluation (Aubinet et al. 2000, Massman and Lee 2002, Baldocchi 2003).

In this study, we compared independent results from model simulations and from observations of the net C gain of the canopy (A) from comparisons with nearby climate stations. Thus, A equals gross primary production (GPP) minus ecosystem respiration (Re) (Ruimy et al. 1995). The forest has been subject to intensive ecosystem research starting almost 40 years ago with the International Biological Programme (Ellenberg 1971). The forest has been subject to intensive ecosystem research starting almost 40 years ago with the International Biological Programme (Ellenberg 1971).

Micro-meteorological site conditions and the first turbulent flux measurements have been described by Laubach et al. (1994). The first long-term turbulent CO₂ fluxes were published by Ibröm et al. (1996). Average energy balance closure varied between 91 and 98% in four years of observation (Aubinet et al. 2000, Ibrom et al. 1996). Average energy balance closure was 91% (Clement 2004).

The Norway spruce (Picea abies (L.) Karst.) forest F1 in the Solling mountains, central Germany, is older than the Griffin Forest (Table 1). Tree density is only one fifth that at Griffin Forest and the trees are taller. In contrast to Griffin Forest, the trees in the Solling F1 Forest form an irregular pattern and vary greatly in crown dimensions and leaf area (Aᵢ). Leaf area index (LAI) is slightly lower at Solling F1 forest than at Griffin Forest. The soil is a 1-m deep dystric cambisol, with few hydromorphic areas. It has not been fertilized apart from the relatively high annual atmospheric nitrogen deposition (> 50 kg N ha⁻¹ year⁻¹) during the last 20 to 30 years (Ibrom et al. 1995). The forest has been subject to intensive ecosystem research starting almost 40 years ago with the International Biological Programme (Ellenberg 1971).

The fetch of the forest exceeds 1.5 km in all wind directions. Forest roads and rides scattered throughout the fetch account for less than 2% of the surface area, thus, flux data are almost never affected by horizontal inhomogeneity. Mean energy balance closure was 91% (Clement 2004).

The stand of Sitka spruce (Picea sitchensis (Bong.) Carr., Queen Charlotte Island provenance) is located in Griffin Forest, near Aberfeldy in central Scotland (Table 1; Valentini et al. 2000, Wingate 2003, Bernhofer et al. 2003, Clement et al. 2003, Clement et al. 2004). Griffin Forest covers 3,862 ha of which about 150 ha form the study area. The stand is situated on a slope facing to WNW (300°) with an inclination of about 4.6°. The soil is a stony, peaty gley, with occasional areas of podsolized cambisol, of 0.7 m depth overlying glacial till. Site preparation consisted of burning and spraying the heather and deep ploughing across the slope. Two lines of trees were planted on the ploughed furrows in an approximate 2 m × 2 m grid. The site has been fertilized with urea (350 kg ha⁻¹, 46% N) once since planting; annual wet and dry nitrogen deposition is about 10 kg N ha⁻¹. During the investigation period (1998), the stand was 17 years old.

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**Material and methods**

**Forest stands**

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**Table 1.** Stand and site characteristics of the study forests. Abbreviation: LAI = leaf area index.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Griffin</th>
<th>Solling F1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>56°37’ N, 3°38’ W</td>
<td>51°46’ N, 9°35’ E</td>
</tr>
<tr>
<td>Elevation</td>
<td>350 ± 20 m</td>
<td>505 m</td>
</tr>
<tr>
<td>Inclination</td>
<td>4.6°</td>
<td>&lt; 1°</td>
</tr>
<tr>
<td>Tree species</td>
<td>Picea sitchensis</td>
<td>Picea abies</td>
</tr>
<tr>
<td>Year planted (tree age at sampling)</td>
<td>1981 (17 years)</td>
<td>1888 (109 + 4 years)</td>
</tr>
<tr>
<td>Tree density</td>
<td>2215 trees ha⁻¹</td>
<td>461 trees ha⁻¹</td>
</tr>
<tr>
<td>Average tree top height</td>
<td>7–8 m</td>
<td>29 m</td>
</tr>
<tr>
<td>Single-sided, projected LAI</td>
<td>7.4</td>
<td>7</td>
</tr>
<tr>
<td>Soil</td>
<td>Podosolized cambisol</td>
<td>Dystric cambisol</td>
</tr>
<tr>
<td>Climate</td>
<td>Maritime</td>
<td>Submaritime/subcontinental</td>
</tr>
<tr>
<td>Average annual air temperature</td>
<td>7.9 °C¹</td>
<td>6.6 °C</td>
</tr>
<tr>
<td>Average annual precipitation</td>
<td>1,400 mm¹</td>
<td>1,045 mm</td>
</tr>
</tbody>
</table>

¹ Climate data estimated from comparisons with nearby climate stations.
cluded that flux data under stable atmospheric stratification and associated with friction velocities ($u_*) < 0.4 \text{ m s}^{-1}$ are affected by the limited fetch at the site (Ibrom 2001). In principle, the two eddy correlation systems were similar. Both used a fast response closed path CO$_2$ and H$_2$O analyzer and a three-dimensional sonic anemometer. Technical details are described in Clement (2004) and Ibrom (1996, 2001).

The study forests grow in different climates, a maritime climate for Griffin Forest and a more continental climate for the Solling F1 stand (Table 1). Although located in different latitudes, the climatic zone is temperate in both cases but both sites are located at transitions between climatic zones: Griffin Forest lies at the transition between the temperate and the boreal zone and the Solling site at the transition from a montane to a subalpine climate. Taking the deep soils and the homogeneous rainfall distribution throughout the year into account, soil water availability is likely sufficient for production throughout the year at both sites.

Parameterization of the forest canopy model MAESTRA

MAESTRA (Medlyn 2004) is the latest version of the forest canopy model MAESTRO (Wang 1988, Wang and Jarvis 1990a, Wang et al. 1990). The main features of MAESTRA are the 3D descriptions of canopy structure and radiative transfer in the canopy, coupled to the physiological responses of leaves at different locations, representing the intra-tree variability.

An objective of our study was to assemble two complete parameter sets to configure MAESTRA for two forest stands using the best current knowledge. The underlying information was obtained from either scientific publications or from unpublished data or reports. The parameters were calculated by nonlinear regression analysis or by algebraic transformation using various statistical procedures in release 8.02 of the statistical analysis system SAS (SAS Institute, Orlando, FL). Acquisition of most parameters followed standard procedures; however, normalization of the $\beta$-functions for leaf area distribution (LAD) and the derivation of the true quantum yields of photosynthetic electron transport ($\alpha_{\text{qs}}$) for spruce needles that make up the complex three-dimensional structure of spruce shoots are described.

Canopy structure description by normalized $\beta$-functions

For Griffin Forest, vertically stratified leaf area data were collected from six sample trees during April 1998 (Wingate 1998). These trees covered three of the most dominant tree classes, with diameters at breast height of 6, 10 and 12 cm. Two branches were collected from four crown heights. From dry mass and specific leaf area measurements, total leaf area of each branch was calculated and extrapolated to the entire whorl in proportion to the number of branches per whorl. Because the positions of the whorls on the sample tree were known, the leaf areas of all whorls, including the unsampled branches, were interpolated with a $\beta$-function (Equation A1) with respect to height. Both the total leaf area of the sample tree and the vertical LAD were determined from the field data. The measured branch lengths were fitted to a half-ellipsoidal crown shape.

Total leaf area, crown height and the function of averaged crown radii at relative crown height were included in Equation A6 to calculate the parameters of the normalized vertical LAD functions by nonlinear least squares minimization. The vertical LADs from the individual trees were weighted by leaf area and then averaged to calculate an average LAD for the stand based on a mean density of 2500 trees ha$^{-1}$ on the sample plots.

For the Solling F1 stand, a 3D crown structure model of a medium-sized Norway spruce tree was used to derive the parameters of the vertical and the radial LAD functions. The mathematical rules for the crown structure model were derived from intensive plant architectural field observations at the site (Kurth and Sloboda 1999). The methods for field measurements and their use in modeling the spatial tree architecture are described by Kurth and Sloboda (1999) and Kurth (1999). The LAD data, which were available at a resolution of 0.016 m$^2$, were used to fit the $\beta$-functions for mature Norway spruce trees in both vertical and radial directions.

Photosynthetic responses to PAR and temperature

In most models, including MAESTRA, leaves are considered to be individually distributed in space, i.e., they are not attached to a shoot, whereas photosynthesis of conifers is usually measured on shoots rather than on single needles. In MAESTRA, shading occurs according to the cumulative leaf areas along the paths of beams of photosynthetically active radiation (PAR) to a simulated point in the crown of a target tree. Absorption of PAR ($Q_p$) and photosynthesis are calculated from incident diffuse and beam radiation at one point considering needle clumping and several leaf inclination angle classes. Because the effects of self-shading have already been considered in the way absorption is calculated by MAESTRA, it is inappropriate to use the photosynthetic response of a shoot rather than of a needle.

The 3D nature of a shoot has two effects on PAR absorption and subsequently on photosynthesis (Stenberg et al. 1995): (1) PAR absorption per unit leaf area of a shoot is reduced through self-shading among different needles and the shoot axis; and (2) the arrangement of needles in shoots causes a broad range of angles between beams and absorbing surfaces. The result is a wide range of PAR photon fluxes ($Q_p$) at the surface of the needles with a lower average than the well-defined $Q_p$ measured by a sensor aligned perpendicular to the plane of a leaf or shoot. Both these effects of shoot structure tend to reduce PAR absorption per unit needle area and thus photosynthetic sensitivity to incident $Q_p$ at the shoot scale.

The problem of how to obtain a single needle photosynthetic response to $Q_p$ from measurements on shoots of complex analytical structure remains to be solved (Wang and Jarvis 1993). Leverenz and Jarvis (1979) prepared Sitka spruce shoots such that needles were arranged in a single layer perpendicular to the incident radiation. Needles were illuminated from the top side. We used their published $Q_p$ response curves (together with the physical conditions reported during their photosynthetic measurements—leaf temperature $16^\circ$C, water vapor pressure deficit ($D$) 700 Pa, [CO$_2$] 300 to 350 $\mu$mol mol$^{-1}$—and a range of stomatal conductances for CO$_2$ trans-
fer as a function of $Q$) to calculate an unbiased true quantum yield ($\alpha_{\infty}$).

Based on generalized optical properties for Sitka spruce needles and the algorithms and parameters for photosynthetic electron transport rate ($J$) used in MAESTRA (Farquhar and von Caemmerer 1982; Equations 16.18 and 16.60), $J$ was calculated for each point of the published light response curves. The initial slopes of non-rectangular hyperbolas of the $J$ versus $Q$, plots, where $Q < 300 \mu$mol m$^{-2}$ s$^{-1}$, were used as estimates of $\alpha_{\infty}$ for shade and sun needles. The convexity parameter of the $Q$ response of $J(\theta)$ could not be estimated from the gas exchange data because measurements were made at ambient CO$_2$ concentration, making it uncertain that electron transport was limiting assimilation at high $Q$. Wang and Jarvis (1993) estimated a $\theta$ of 1; however, a pure Blackman response curve is unrealistic for needles illuminated predominantly from one side, because chloroplasts tend to shade each other in a needle (Stenberg et al. 1995). In the absence of a better value, we set $\theta$ for both species to 0.8 in the simulations and in the estimations of $\alpha_{\infty}$.

Maximum rates of electron transport ($J_{\text{max}}$), carboxylation ($V_{\text{max}}$) and dark respiration were taken from field measurements in a Sitka spruce plantation of similar age (Barton 1997, Meir et al. 2002) and from a 3-week campaign in 1997 at the Solling F1 site where we measured current-year and 1- and 2-year-old twigs on detached branch systems (see Lange et al. 1986) sampled from the sun, intermediate and shade crown as defined by Fuchs et al. (1977) with an air-conditioned cuvette system (CMS 400, Walz Effeltrich, Germany). In both sets of field measurements, relationships between biochemical parameters and leaf traits, such as leaf nitrogen concentration and specific leaf area, were investigated with the intention of using them to scale up the leaf-level measurements to entire tree crowns. However, except for dark respiration, the relationships to leaf nitrogen were weak; therefore, we used mean values for $V_{\text{max}}$ and $J_{\text{max}}$. Parameter values at a reference temperature of 25 °C are listed in Table 2.

The $V_{\text{max}}$ estimate for Norway spruce was similar to that given by Falge et al. (1996), whereas $J_{\text{max}}$ was only two thirds of their estimate. The $J_{\text{max}}/V_{\text{max}}$ ratio of 1.7 compared well with values from temperate coniferous forests summarized in Wullschleger (1993) but was lower than the values compiled for Picea abies (Wulischlger 1993, Falge et al. 1996).

Temperature responses of photosynthetic biochemical parameters for the Solling Norway spruce were fitted to gas exchange measurements in the leaf temperature range between 8 and 25 °C following De Pury and Farquhar (1997):

\[
V_{\text{max}} = V_{\text{max},0} e^{\frac{E}{R T}},
\]

where parameter $E_{V_{\text{max}}}$ = 56,000 J mol$^{-1}$ and $R$ is the universal gas constant. The temperature response of $J_{\text{max}}$ was:

\[
J_{\text{max}} = J_{\text{max},0} e^{\frac{E_{J_{\text{max}}}(T_{\text{r}}-T_{\text{r}})}{R T} - \frac{\Delta S}{R} - \frac{\Delta S T}{R T} - \frac{\Delta S T}{R T} - \frac{\Delta S T}{R T}}
\]

where parameters $E_{J_{\text{max}}}$, $E_{J_{\text{max}}}$ and $\Delta S$ have values of 40,000 J mol$^{-1}$, 220,000 J mol$^{-1}$ and 710 J K$^{-1}$ mol$^{-1}$, respectively. Temperature dependency of dark respiration rates ($R_d$) was described by:

\[
R_d = R_{d,0} e^{c(T_{\text{r}}-T_{\text{r}})}
\]

where parameter $c$ = 0.083 K$^{-1}$.

In Equations 1–3, subscript $r$ indicates that data are related to the reference temperature ($T_{\text{r}}$) of 298 K. Although the dependence of Sitka spruce photosynthesis on temperature was well defined by Neilson et al. (1972), dependencies of the photosynthetic biochemical parameters on temperature have not been measured explicitly and were assumed to be similar to those for Norway spruce at the Solling stand.

### Stomatal conductance
A set of empirical equations was used to relate stomatal conductance ($g_s$) to incoming $Q$, leaf temperature, ($T_l$), CO$_2$ concentration and D (Jarvis 1976). The single factor equations were normalized and combined by multiplying each with the maximum stomatal conductance in one

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Intercept $\pm$ SE (µmol m$^{-2}$ s$^{-1}$)</th>
<th>Slope $\pm$ SE (µmol gN$^{-1}$ s$^{-1}$)</th>
<th>$r^2$</th>
<th>$n$</th>
<th>Range in the canopy or mean $\pm$ SE (µmol m$^{-2}$ s$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sitka spruce (after Meir et al. 2002)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$R_d$</td>
<td>$-0.7 \pm 0.4$</td>
<td>$0.9 \pm 0.2$</td>
<td>0.52</td>
<td>23</td>
<td>1.0 to 1.3</td>
</tr>
<tr>
<td>$V_{\text{max}}$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$J_{\text{max}}$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Norway spruce</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$R_d$</td>
<td>$-0.6 \pm 0.4$</td>
<td>$0.8 \pm 0.1$</td>
<td>0.79</td>
<td>13</td>
<td>2.0 to 3.5</td>
</tr>
<tr>
<td>$V_{\text{max}}$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$J_{\text{max}}$</td>
<td></td>
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</tr>
</tbody>
</table>

**Table 2.** Biochemical photosynthesis parameters and their standard errors (SE) for Sitka spruce and Norway spruce at a reference leaf temperature of 25 °C. Regression parameters are derived from regressions between dark respiration rates ($R_d$) and leaf nitrogen (N) concentration per unit leaf area. Abbreviations: $V_{\text{max}}$ = maximum rate of carboxylation; $J_{\text{max}}$ = maximum rate of electron transport; and $n$ = number of samples.
multi-factorial, nonlinear equation.

Single response functions for Sitka spruce twigs were taken from the literature. To combine these functions measured by different authors at different sites and times into the full model we assumed that both functions and parameters are universal among Sitka spruce trees of the same provenance in Scotland. Sandford and Jarvis (1986) measured maximum stomatal conductance \( g_{s_{\text{max}}} \) at increasing \( D \) in 12-week-old shoots of 3-year-old potted plants in a greenhouse. The response function for \( g_s \) to \( D \) given by Sandford and Jarvis (1986, Equations 3 and 4) rearranged to the general form that is used in MAESTRA is:

\[
g_s = g_{s_{\text{max}}}/(1 + D/D_{0.5})
\]

where constant \( D_{0.5} \) equals 375 Pa for Sitka spruce and can be interpreted as the value of \( D \) at which \( g_s \) is reduced by 50% of \( g_{s_{\text{max}}} \). The low \( D_{0.5} \) value indicates high sensitivity of Sitka spruce stomata to moderate values of \( D \). Maximum stomatal conductance was calculated from branch-bag measurements at the Griffin Forest (Wingate 2003) and cuvette measurements by Barton (1997), which confirmed earlier values from Fetteresso Forest (Watts et al. 1976, Beadle et al. 1979). From these maximum values of about 0.15 mol m\(^{-2}\) s\(^{-1}\), the theoretical parameter \( g_{s_{\text{max}}} \) of 0.24 mol m\(^{-2}\) s\(^{-1}\) was calculated for \( D_{\text{lim}}=0 \) with Equation 4. MAESTRA uses \( g_s \) for CO\(_2\) rather than for \( H_2O \), i.e., 0.154 mol m\(^{-2}\) s\(^{-1}\) for CO\(_2\). The parameters of the temperature response function (–5, 15 and 40 °C for minimum, reference and maximum temperatures, respectively) were calculated from Neilson and Jarvis (1975, Figures 1, 4 and 5) from shoots at Fetteresso Forest in 1969–1970 (Table A1). Stomatal response to incident \( Q \) and to external CO\(_2\) concentration was taken from Jarvis (1976) and Barton (1997) respectively (Table A2).

The Norway spruce parameter set was derived from 470 single measurements made in situ by Olchev et al. (1997) with a steady-state porometer at the Solling F1 site. We used the full model to derive the parameters by nonlinear least squares minimization. The single values were weighted inversely to their abundance in a 2D variable space, defined by the leaf temperature and \( D \) ranges, to reduce the effects of the generally strict correlation between these two environmental variables in ambient conditions. Parameter estimates are listed in Table A2.

The empirical model explained only one quarter of the observed variability in \( g_s \). Spatial variability in \( g_s \), resulting from the effects of acclimation to shade on \( g_{s_{\text{max}}} \), which has been neglected here, may account for the high noise in the measured data. Also not taken into account is the effect of leaf water potential on \( g_s \). In the original model, Jarvis (1976) included stomatal response to leaf water potential and was able to explain 51% and 75% of \( g_s \) variation for Sitka spruce and Douglas fir, respectively. Inclusion of this effect might reduce the unexplained variance in the Norway spruce data set.

**Simulations**

The significant differences between canopy structures of the study forests reflect not only species-specific differences, but also differences in stand age and history. Tree distribution at Griffin was derived from measurements made in 1998 (Figure 1a). The simulated 30 × 30 m\(^2\) sample plot contained 225 identical trees each with a leaf area of 33.3 m\(^2\). Because the radial LAD distribution was not measured in the tree samples from the Griffin Forest, the parameters were taken from the Cloich experiment (Sinclair 1995). A tree in the center of each sample plot was selected as the target tree for simulations. Because the virtual trees and their environment were identical, this tree was representative for the whole cohort. For the Solling F1 stand, the trees were arranged on the basis of a measured 30 × 30 m\(^2\) tree map with individual tree heights, crown radii and total leaf areas (Figure 1b). The surrounding area was filled by trees with averaged crown properties on a regular grid basis to provide appropriate boundary conditions. The grid size was chosen to maintain a tree density of 461 trees ha\(^{-1}\), the tree density of the Solling F1 stand at the time of investigation. Because the trees in the Solling F1 stand were older, they differed greatly one from another, so the simulation was done for a set of 28 target trees (see Figure 1b). Tree structure was described by a general 2D \( \beta \)-function but the crown dimensions and total leaf area assigned were tree-specific. The simulation results at the tree scale were then used to calculate simulated stand \( P_s \), with stand LAI as a scaling factor.

**Weather during the observation period**

At both sites, simulations were driven by half-hourly meteorological data covering a 3-month period in summer 1998 (Table 3). The weather during the simulation period was similar at the two sites. However, at the Griffin site, the oceanic influence was evident as a lower seasonal temperature, a slightly lower \( D \), a lower \( Q \) and a lower averaged beam fraction (\( f_b \); defined as fraction of beam radiation in total incident PAR) relative to the Solling site. The longer day length (1 h) at Griffin than at Solling was compensated by lower potential \( Q \) and by more cloudiness. The empirical description of \( f_b \) (Spitters et al. 1986) used in MAESTRA was only roughly confirmed by observations with shaded and unshaded pyranometers at the Solling F1 site. Diffuse irradiance differed by < 7% between sites. Higher mean \( Q \) at the Solling site was mainly a result of the almost 2-fold higher flux of beam \( Q \). Mean daily temperature and consequently \( D \) amplitude were similar at the study sites.

**Preparation of the turbulent carbon dioxide flux data**

Under conditions satisfying the assumptions of the derivation of the turbulent flux equation, turbulent CO\(_2\) fluxes measured at a point well above the forest canopy (\( F_c \)) can be assumed to represent net ecosystem CO\(_2\) exchange (cf. Stull 1988, Kaimal and Finnigan 1994). The general non-systematic error of turbulent flux measurements is at least 10–20% (Wesely and Hart 1985) but can be much larger and become systematic be-

The sum of $F_c$ and the rate of CO$_2$ storage change in the air column below the eddy correlation system represents the net biotic flux ($F_b$)—the net balance of $R_E$ and $P_g$. To estimate $P_g$ and $R_E$, the remaining $F_b$ data were separated into nighttime and daytime values.

Half-hourly data of nighttime $F_b$ were selected according to variable $u_*$ thresholds and used to derive several nonlinear temperature dependencies of $R_E$:

$$R_E = R_0Q_{10}^{\frac{T}{10}}$$

where $T$ is temperature in °C and $Q_{10}$ and $R_0$ are empirical parameters. These parameters cannot be directly compared with physiological parameters, because they integrate over different sources, i.e., microbial and tree respiration. Their relative contributions to $R_E$ may vary with time and with temperature, which has an effect on the parameter values. We used both air temperature and soil temperature (at 5-cm depth) when considering the different sources of respired CO$_2$. To consider possible seasonal changes in the temperature dependencies of $R_E$ we used flux data sets either from the entire 3-month observation period or from each month separately. Temperature dependencies of nighttime $F_b$ were also used to estimate $R_E$, thereby allowing extrapolation from nighttime over the day and over periods when nighttime data were rejected or missing. Applying all calculation schemes, i.e., monthly and 3-monthly temperature fits with either soil temperature or air temperature, yielded four ways to estimate $R_E$. For each site, all schemes were applied to flux data sets that had been selected according to eight $u_*$ thresholds ranging from 0 to 0.7 m s$^{-1}$.

### Table 3. Weather conditions in the 3-month summer period (May 1–July 31, 1998) used as input for the simulations. Beam fractions were calculated after Spitters et al. (1986) as in MAESTRA and weighted by $Q$. Abbreviations: $D =$ water vapor pressure deficit; and $Q =$ photon flux densities.

<table>
<thead>
<tr>
<th>Weather element</th>
<th>Griffin</th>
<th>Solling F1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temperature (°C)</td>
<td>Mean</td>
<td>9.8</td>
</tr>
<tr>
<td></td>
<td>Mean daily amplitude</td>
<td>2.6</td>
</tr>
<tr>
<td>$D$ (Pa)</td>
<td>Mean</td>
<td>329</td>
</tr>
<tr>
<td></td>
<td>Mean daily amplitude</td>
<td>242</td>
</tr>
<tr>
<td>$Q$ (µmol m$^{-2}$ s$^{-1}$)</td>
<td>Mean day time values only</td>
<td>443</td>
</tr>
<tr>
<td></td>
<td>Mean maximum (mean potential)</td>
<td>681 (1697)</td>
</tr>
<tr>
<td></td>
<td>Mean diffuse</td>
<td>340</td>
</tr>
<tr>
<td></td>
<td>Mean beam</td>
<td>103</td>
</tr>
<tr>
<td>Weighted mean beam fraction (%)</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>Mean day length (h)</td>
<td>16.8</td>
<td></td>
</tr>
<tr>
<td>Mean wind speed (m s$^{-1}$)</td>
<td>2.8</td>
<td></td>
</tr>
</tbody>
</table>

Figure 1. Tree distribution at Griffin Forest (a) and Solling F1 (b). Trees with no numbers in panel B have average properties and were included only as boundary conditions around the model section.
Finally, $P_g$ was calculated as the difference between $F_g$ and $R_g$ or set to zero in the dark. All of these methods carry the risk of propagating nighttime errors to the $P_g$ estimate. Any underestimation of daytime $R_g$ will lead to an underestimation of $P_g$. Although $P_g$ is a calculated flux which cannot be measured directly, this estimate is dominated by the measured turbulent flux data. For simplicity, these data are further referred to as observed data to distinguish them from simulated $P_g$. The use of the term “observed” does not imply a more realistic estimation of $P_g$; both estimations are prone to errors as will be discussed in the context of the comparisons we made.

Results

Crown structures of the spruce forests

Vertical LAD distribution functions of five trees of Griffin Forest were calculated from biometric field data (Wingate 2003). Mean leaf area reached 34.8 m² tree⁻¹. Although there were large differences between individual trees, leaf area was always concentrated in the lower parts of the crown (Figure 2). The older Solling F1 trees had a mean leaf area of 152 m² tree⁻¹ and vertical LAD distribution was more symmetric than in the Griffin trees with a maximum LAD at 60% of crown height (Figure 2). The crowns of the Solling trees were nearly twice as long and wide as those of the Griffin trees but maximum LAD was only one half that of the Griffin trees. During development, a transition zone formed below the shade crown in the taller and older Norway spruce stand where branches started to shed their needles and gradually died back, leading to a trunk space below the crowns. By contrast, the younger Sitka spruce stand had live branches to the ground. The extreme LAD in the lower canopy was a consequence of recent canopy closure and the relatively high tree density. Figure 2 includes data from other sites for comparison. Two general trends emerge from these data. First, aging leads to a more symmetrical vertical LAD function and, second, a higher stocking density leads to a narrower vertical LAD function. Comparing vertical leaf area distributions of mixed broad-leaved deciduous forests of different ages, Baldocchi et al. (2002) found an even more pronounced concentration of leaf area near the top of the crowns with stand age. Thus, relationships between leaf area density distributions and stand age are species, stocking density and life form dependent, and can be altered by nutrient and water availability (Wang et al. 1990).

Horizontal LAD distribution was calculated for the Solling F1 trees only because there were no appropriate data available for the Griffin trees. Some published normalized 2D $\beta$-functions for Sitka spruce were used for comparison (Figure 3). Figure 3d shows that needles inside the crowns of the Solling F1 trees were more homogeneously distributed compared with the younger Sitka spruce stands, a result of branch development from dormant epicormic buds into the inter-whorl stem sections. The larger radial concentration of needles towards the center of the crowns of the Sitka spruce stands may be a consequence of the high tree density leading, in turn, to contact zones between the crowns in which the branch tips overlap (cf. Figures 1a and 1b). Despite similar LAI, the canopy structures of the forests differed substantially.

Quantum yields of photosynthetic electron transport

Previous versions of MAESTRA treated the initial slope of the $J$–$Q_a$ relationship as a universal constant with a default value of 0.425 mol e⁻ mol⁻¹ absorbed PAR following Evans and Farquhar (1991). This high value was not supported by empirical evidence, in the case of the two study species. Mean values of 11 simulations in which the external CO₂ concentration was increased from 300 to 350 µmol mol⁻¹ in steps of 5 µmol mol⁻¹ yielded $\alpha_e$ estimates of 0.36 (0.004 standard deviation) and 0.28 (0.003) mol e⁻ mol⁻¹ absorbed PAR for shade and sun crown branches, respectively. The mean standard error of the nonlinear parameter estimation was 0.02 mol e⁻ mol⁻¹ absorbed PAR for shade-crown needles. The degrees of freedom were too small to calculate a value for the sun crown. Assuming a 60% proportion of the sun crown leaf area, the mean value of $\alpha_e$ was 0.32 mol e⁻ mol⁻¹ absorbed PAR with an estimated standard error of about 6%.

Leverenz (1987) published apparent quantum yields of 0.057 mol CO₂ mol⁻¹ PAR in shade-adapted Norway spruce needles that had been prepared in the same way as described for the Sitka spruce shoots. Photosynthesis was measured at ambient CO₂ concentrations and needles were illuminated from the top. Because stomatal conductances were not reported, we used the stomatal conductance sub-model of
MAESTRA in the calculation of $J$ from the measured CO$_2$ uptake rates and the reported ranges of leaf physical conditions throughout their measurements. The resulting value of $\alpha_{e-}$ was 0.33 (0.003) mol e$^{-}$ mol$^{-1}$ absorbed PAR, only slightly less than in shade-adapted Sitka spruce needles. No $Q$ response data for needles from the sun-crown are available, but in situ CO$_2$ and H$_2$O gas exchange measurements in a 1-year-old shoot from the lower sun crown confirmed our calculations for the Solling F1 Forest (Oleg Panfyorov, Institute of Bioclimatology, University of Goettingen, Germany, unpublished data). The mean $\alpha_{e-}$ deemed representative for the entire crown was 0.3 mol e$^{-}$ mol$^{-1}$ absorbed PAR.

Although errors in the calculations of $J$ from photosynthetic rates due to uncertainties in leaf physical conditions during the measurements were relatively small, the error in the estimates might be much larger because of physiological variability among needles within tree crowns and differences between the measured trees and the simulated stands. The standard error estimate of 6% is, therefore, to be interpreted as a minimum standard error of $\alpha_{e-}$.

Both calculated $\alpha_{e-}$ values are much lower than the theoretical value of 0.425 mol e$^{-}$ mol$^{-1}$ absorbed PAR reported by Evans and Farquhar (1991) and lower than the value of 0.38 mol e$^{-}$ mol$^{-1}$ absorbed PAR calculated from the data of Long et al. (1993), who measured photosynthesis in Norway spruce shoots at low oxygen concentration in a light integrating sphere. The $\alpha_{e-}$ values are also somewhat lower than the value of 0.36 mol e$^{-}$ mol$^{-1}$ absorbed PAR that was derived from modeling the illumination of Sitka spruce needles in a shoot exposed to a bi-directional light source (Wang and Jarvis 1993). However, our estimates are similar to values reported for some broad-leaved C$_3$ plants measured at low oxygen concentration (Ehleringer and Björkman 1977) and the mean value that was derived from measurements made by Singsaas et al. (2001).

**Sensitivity analyses**

Gross canopy photosynthesis and PAR absorption to leaf area distribution  Wang and Jarvis (1990b) investigated the sensitivity of photosynthesis, PAR absorption and transpiration to the way LAD distribution in Sitka spruce trees was modeled in MAESTRO. For a thinned Sitka spruce stand (1500 trees ha$^{-1}$) they found that, over the range of LAI from 0.75 to 12, PAR absorption was always higher for a uniform LAD distribution than for a 2D LAD distribution. For LAI < 6, net photosynthesis was higher, for LAI > 7 it was lower for the
uniform LAD distribution than for the 2D LAD distribution. We investigated the effects of the three LAD distributions on the simulated PAR absorption and $P_g$ in the two study stands. Because a horizontal LAD distribution was not available for Griffin, data from comparable trees in the Cloich stands were used. Results are summarized in Table 4.

In the three simulations for each site, all parameter values except those determining the LAD distributions were kept constant; i.e., the simulations differed only in the way the leaf area inside the tree crowns was more or less clumped. In a solitary tree, clumping of needle area increases from uniform for 1D LAD distribution and is maximal at 2D LAD distribution; however, the situation at the stand scale is more complex because crowns may overlap and shade one another. The overall effects of the LAD parameterization on simulated $P_g$ and $Q_a$ were larger for the Solling canopy than for the Griffin canopy, where both gap size and total projected gap area between crowns were smaller (cf. Figure 1) and relative PAR absorption was larger.

Differences in simulated $Q_a$ and $P_g$ between the three simulations of the less dense Solling canopy were comparable with those predicted at the single tree scale. The more uniform the distribution of LAD in the tree crowns the larger were $Q_a$ and $P_g$. In contrast, in the Griffin stand, simulated $Q_a$ was higher with the 1D LAD distribution than with the uniform LAD distribution and $P_g$ was lower in the simulation with the 1D LAD distribution than with the 2D LAD distribution (Table 4). The reasons for this difference are associated with the individual canopy structure of the Griffin stand, where larger parts of the crowns overlapped, gaps in the canopy were small and leaf area was more concentrated in the inner and lower crown parts than in the Solling canopy (cf. Figures 2 and 3). Neglect of the radial heterogeneity of LAD in the tree crowns led to artificially high leaf area concentrations in the overlapping crown zones. The effects were lower in the simulations with uniform LAD distribution because the leaf area was shifted upward in the canopy where the gap size was larger and shading between trees less.

It can be concluded from the sensitivity analyses that the type of LAD distribution affects the simulation of $Q_a$ and $P_g$ in the range of a few percents up to 12%. The effect the parameterization of LAD distribution taken in the simulation depends on canopy traits like tree density, crown dimensions and relative absorptance. The two simplified parameterizations that neglected horizontal heterogeneity in LAD distribution introduced artefacts in the description of the canopy structure, to which the simulation was sensitive, indicating the need to use the 2D LAD distribution for simulations of dense forest canopies.

Gross canopy photosynthesis and the true quantum yield A range from 0.2 to 0.425 mol CO$_2$ mol$^{-1}$ e$^{-}$ was used in simulations at both sites to define the relative sensitivity of $P_g$ to $\alpha_{e}$, expressed as the rate of change of simulated $P_g$ per unit change of $\alpha_{e}$ relative to the reference $\alpha_{e}$. A small nonlinearity existed in the relationship between relative $P_g$ and $\alpha_{e}$. Averaged relative sensitivities amounted to 1.6 (± 0.3) mol e$^{-}$ mol$^{-1}$ CO$_2$ for Griffin and 1.9 (± 0.3) mol e$^{-}$ mol$^{-1}$ CO$_2$ for the larger Solling trees. Given a minimum uncertainty in the parameter $\alpha_{e}$ of ± 6%, the minimum accuracy of the simulation results is in the order of ± 3%. If the theoretical $\alpha_{e}$ value of 0.425 mol CO$_2$ mol$^{-1}$ e$^{-}$ were used, simulated $P_g$ would be 14 and 21% higher than for the reference simulation for Griffin and Solling, respectively.

Gross canopy photosynthesis and combinations of the true quantum yield and leaf clumping The sensitivity of the model to variation in $\alpha_{e}$ and a needle clumping indicator ($I_c$; ratio of the projected shoot area to the projected needle area of all needles in a shoot) was investigated. We selected $I_c$ because it affects $P_g$ through the calculation of $Q_a$ in the model. A higher $I_c$ value, i.e., a smaller degree of needle clumping, leads to more PAR absorption per unit leaf area. A reference value for $I_c$ of 0.7 was adopted (cf. Wang and Jarvis 1990b).

In Figure 4, simulated $P_g$ is shown as depending on the combination of the two model parameters for the Sitka spruce stand. At the shoot scale, positive correlations of $\alpha_{e}$ and $I_c$ with $P_g$ can be assumed because an increase in both parameters should increase $P_g$ at constant $Q$. Results at the canopy scale showed, however, that $P_g$ was positively correlated only with $\alpha_{e}$, whereas it was negatively correlated with $I_c$.

To understand the different effect of $I_c$ at canopy scale compared with the shoot scale, consider that PAR distribution in the canopy is also affected by needle clumping. Large values of $I_c$ result in large effective extinction coefficients; i.e., PAR absorption per unit leaf area increases in the upper canopy layers at the expense of PAR absorption deeper in the canopy. Because of the nonlinear response of $P_g$ to $Q$, the sensitivity of $P_g$ to $Q$ is lower at high $Q_a$ than at low $Q_a$. Large $I_c$ (i.e., less clumping) leads to a relatively small increase in $P_g$ in shoots in the upper canopy but to a relatively large decrease in $P_g$ deeper in the canopy. These relationships might explain the negative correlation between $I_c$ and $P_g$ of the entire canopy.

The two additional lines in Figure 4 show those combinations of $\alpha_{e}$ and $I_c$ that would lead either exactly to the average $P_g$ in the reference simulation or exactly to the average $P_g$ that was calculated from the flux measurements. The examples illustrate that the same simulation result can be achieved with different combinations of the two model parameters and, most

Table 4. Sensitivity of gross photosynthesis rates ($P_g$) and photosynthetically active radiation absorption rates ($Q_a$) to different leaf area distributions in the simulation. Abbreviations: UD stands for uniform; 1D for one dimensional vertical; and 2D for two dimensional vertical and radial leaf area density distributions.

<table>
<thead>
<tr>
<th>Relative effect</th>
<th>Griffin</th>
<th>Solling</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Q_a$(1D)/$Q_a$(2D)</td>
<td>1.05</td>
<td>1.05</td>
</tr>
<tr>
<td>$Q_a$(UD)/$Q_a$(2D)</td>
<td>1.03</td>
<td>1.12</td>
</tr>
<tr>
<td>$P_g$(1D)/$P_g$(2D)</td>
<td>0.98</td>
<td>1.05</td>
</tr>
<tr>
<td>$P_g$(UD)/$P_g$(2D)</td>
<td>1.03</td>
<td>1.06</td>
</tr>
</tbody>
</table>
likely, many other parameter combinations as well. This phenomenon is generally called equifinality (Franks et al. 1997) and is a consequence of model over-parameterization.

Comparison of simulated carbon uptake with measured turbulent CO$_2$ fluxes

Observed CO$_2$ fluxes The various $R_E$ estimations showed that both temperature-normalized $R_E$ and the relationship between observed and simulated $P_g$ stabilized at a $\alpha_e$ threshold of 0.5 m s$^{-1}$. Below this threshold, normalized $R_E$ increased steadily at the Solling site, whereas it remained largely unaffected by any $\alpha_e$ threshold at the Griffin site. Here, low turbulent mixing was associated with higher random scatter of normalized $R_E$ values. We treated both data sets equally and set the $\alpha_e$ threshold at 0.5 m s$^{-1}$ for both sites.

Allowing for monthly seasonality in temperature response of $R_E$ did not greatly affect either the sum of $R_E$ over the entire period (differences < 1%) or the relationships between observed and simulated $P_g$. Therefore, we used the 3-month regressions for our comparisons.

Use of soil temperature instead of air temperature in the calculation reduced estimated $R_E$ on average by 11.8 and 8.8% for Griffin and Solling, respectively, perhaps reflecting that daytime air temperatures were significantly higher than nighttime air temperatures (on average 2.2 and 1.6 °C for Griffin and Solling, respectively), whereas these differences were much smaller for soil temperatures (< 0.2 °C at both sites). Thus, use of air temperatures increased daytime $R_E$ over the measured nighttime $F_N$, whereas use of soil temperatures did not lead to this increase.

Which temperature should be used is a matter of interpretation. Soil and aboveground canopy respiration can be assumed to be of similar magnitude in these sites (Janssens et al. 2001). Unless using a better model that includes temperature distribution in the forest and individual temperature coefficients for respiration in the different tissues or soil strata, both estimations are equally justified. Consequently, the observed difference is a measure of an inherent systematic error in $R_E$ and $P_g$ when calculated from measured $F_N$ only. The relative effect on $P_g$ was smaller, –7.7% and –5.2% for Griffin and Solling, respectively, because the absolute magnitude of $P_g$ compared with $R_E$ was larger. In the following comparisons we used $P_g$ estimates based on air temperatures.

Both forest stands took up C from the atmosphere throughout the 3-month study period. Calculated net CO$_2$ uptake rate of the mature Norway spruce stand, 202 g C m$^{-2}$ over 3 months, was much smaller than that of the young Sitka spruce plantation, 341 g C m$^{-2}$ over 3 months. The $P_g$ reached 794 g C m$^{-2}$ over 3 months in the Norway spruce stand and 996 g C m$^{-2}$ over 3 months in the Sitka spruce plantation. Despite the larger tree biomass, ecosystem respiration was only 592 g C m$^{-2}$ over 3 months in the Norway spruce stand compared with 656 g C m$^{-2}$ over 3 months in the Sitka spruce plantation, indicating that ecosystem respiration is an indicator of higher heterotrophic respiration rates in the young Sitka spruce plantation. All CO$_2$ flux rates were lower in the mature Norway spruce stand; however, although $P_g$ and $R_E$ differed by only 20 and 10%, net uptake was 40% lower in the Norway spruce stand than in the Sitka spruce stand.

Simulated versus observed CO$_2$ uptake We conducted studies to determine if MAESTRA was able to simulate the different biophysical behavior of the two forest stands. In contrast to $F_N$, observed $P_g$ can be directly compared with the results of MAESTRA. The observed and simulated estimates of $P_g$ were completely independent of one other. In the following regression analyses, we chose the variable with the smallest variation (simulated $P_g$) as the “independent” variable. Averaged diurnal course and simulated and observed mean $P_g$ were used for further comparisons.

Results from the Griffin Forest stand are shown in Figures 5a and 5b and indicate that 91% of the variation in observed $P_g$ could be explained by covariance with simulated $P_g$ in the Sitka spruce plantation. The regression line differed by < 6% from the one-to-one line (Figure 5a). During daytime, the residual scatter was more or less homogeneously distributed around the regression line with a standard deviation of 3.7 µmol m$^{-2}$ s$^{-1}$. A small part of the unexplained variability may be attributed to phenological development, which was not considered in the parameterization of MAESTRA. The slopes of monthly regressions between simulated and observed $P_g$ varied moderately with values of 1.06, 1.01 and 1.13 for May,

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**Figure 4.** An example of equifinality in simulated gross photosynthesis ($P_g$) of the Griffin Forest: isolines describe identical values of simulated $P_g$ in µmol m$^{-2}$ s$^{-1}$ that were averaged over a 3-month simulation period. The simulations used different combinations of the physiological parameter “quantum yield of photosynthetic electron transport,” ($\alpha_e$) and a clumping indicator describing structural effects on photosynthetically active radiation (PAR) absorption. The observed $P_g$ was 10.4 µmol m$^{-2}$ s$^{-1}$ and the simulated $P_g$ using initial parameters was 9.8 µmol m$^{-2}$ s$^{-1}$; both were averaged over the three month simulation period.
June and July. Their standard errors were slightly larger than 0.01.

Results from the Norway spruce stand also showed good agreement between simulated and observed $P_g$ (Figure 5c). The regression analysis revealed a slightly larger (10%) simulated $P_g$ than observed $P_g$. As with the Griffin simulations, the slopes varied slightly, indicating a better fit in June and July ($1.01 \pm 0.009$ and $0.97 \pm 0.008$) than in May ($0.87 \pm 0.009$). A small overestimation of $P_g$ by the model at low $Q$ might have been caused by the use of a quantum yield derived from measurements on shade-crown shoots. As in the Griffin stand, there was considerable scatter around the regression line with a standard deviation of 3.8 µmol m$^{-2}$ s$^{-1}$. The origin of the scatter may be attributable to real flux variability and to errors both in the model and in the turbulent flux measurements. If the generalized error estimate for turbulent flux measurements given by Wesely and Hart (1985) is applicable to the site and measurement conditions at the two study sites, random error can easily account for the observed unexplained variability in the regressions (Figures 5a and 5c). Additional bias in the observed $P_g$ might have been caused by errors in the nighttime $R_0$ measurement and its extrapolation over daytime. However, the simulated results may be erroneous because of uncertainty in parameterization or use of oversimplifying assumptions in the model structure. Assuming that bias in the meteorological input data was low, it can be expected that errors associated with the model will tend to be of a more systematic than random nature, because both model structure and parameters were constant over the simulations. Thus, the scatter in the comparisons was most likely introduced by the turbulent flux data and not by the model output.

The simulated mean diurnal course of $P_g$ followed closely its corresponding observed course (Figure 5d) and the means over the entire period differed by only 5% with 10.4 µmol m$^{-2}$ s$^{-1}$ and 9.9 µmol m$^{-2}$ s$^{-1}$ for observed and simulated $P_g$, respectively. During the noon period (1100–1400 h), simulated $P_g$ was on average 7% lower than observed $P_g$, indicating that either the photosynthetic capacity was not high enough in the model or that the observed $P_g$ was systematically too high under these conditions. At saturating $Q$, photosynthetic capacity can be assumed to be limited by $V_{\max}$. This parameter had a 17% lower value for Sitka spruce than was used for Norway spruce (Table 2). Keeping all other parameters as in the reference simulation, the best fit between simulated and observed
$P_g$ was achieved with a $V_{\text{max}}$ of 43 µmol m$^{-2}$ s$^{-1}$, the value used in the simulations of the Solling stand.

In contrast to the Griffin stand, the systematic differences between simulated and observed $P_g$ at the Solling stand were confined to the afternoon, whereas during the rest of the day the estimates were similar (Figure 5d). Observed mean daily $P_g$ was 8.3 µmol m$^{-2}$ s$^{-1}$ and the corresponding simulated estimate was 8.5 µmol m$^{-2}$ s$^{-1}$; these estimates differed by only 2.4%. The small apparent overestimation by the model during the afternoon coincided with the time of largest $D$, i.e., the time of day when atmospheric demand for transpiration was maximal. A possible explanation for the systematic differences between observed and simulated $P_g$ that was not adequately represented by the model.

To identify systematic differences between simulated and observed $P_g$, analysis of residuals was applied with respect to time and $Q$, $T_a$, $D$ and $f_b$. For both stands, residuals of the regression were not distributed stochastically in time (not shown). On some days, simulated $P_g$ was systematically either higher or lower than observed $P_g$, whereas the two estimates matched almost perfectly during other days. Comparison with the meteorological data showed that the residuals were negative especially when both $D$ and radiation were high (Figures 6b and 6d). Usually, these weather conditions occurred together with high $f_b$ and high $T_a$. Because the four weather elements were more or less correlated with one another, it is difficult to distinguish the particular effects of any one of these on $P_g$ from field measurements. In general, the residuals were satisfactorily symmetrically distributed.

There are at least two reasons for negative residuals in sunny conditions: one is unexpected extreme closure of stomata in the stand as a direct response to moderately large $D$, resulting in stomatal limitation of photosynthesis. Stomata of spruce species are quite sensitive to atmospheric $D$. However, underestimated observed $P_g$ could also cause systematic differences from simulated $P_g$. Underestimation of daytime soil respiration, for example, would lead to underestimation of observed $P_g$. Under conditions of extreme turbulence, often associated with fair weather conditions, vertical entrainment of CO$_2$ from the soil through “pressure pumping” (Massman and Lee 2002) might lead to a higher CO$_2$ efflux from the soil than can be expected from the extrapolated nighttime $R_e$. Under extreme convective turbulence, Taylor’s frozen turbulence hypothesis may not perfectly apply (Stull 1988), resulting in a loss of covariance and, hence, net flux signal. All these possible examples, and several others, could cause the negative residuals in Figures 6b and 6d at high $f_b$ and $D$.

Figure 6. (a,c) Response of canopy photosynthesis ($P_g$) to photosynthetically active radiation (PAR). The arrows indicate saturation of simulated $P_g$. (b) Residuals from the regression analysis (see Figures 5a and 5c) over vapor pressure saturation deficit ($D$) at Griffin Forest (a,b) and Solling F1 (c,d). Abbreviation: $Q$ = PAR photon flux.
Differences between forests in photosynthetic light response

Our analyses showed that $P_g$ observations contain both random scatter and biological response to $Q$ and to other weather elements. At high $Q$, scatter and biological response to factors other than $Q$ in the turbulent flux data are of the same order of magnitude. At low $Q$, statistical noise in observed $P_g$ was of the same order of magnitude as the total variability in simulated $P_g$, including its $Q$ response. Therefore, classical analysis of the photosynthetic $Q$ response becomes difficult when using $P_g$ estimates based on measured turbulent CO$_2$ flux data. Simulated $P_g$ showed no such scatter and any variability in simulated $P_g$ was caused by a combination of the simulated processes. Therefore, we investigated the simulated light response of photosynthesis and interpreted it as one possible explanation for the differences in observed $P_g$ between the two forest canopies.

MAESTRA was generally able to construct the principal responses of $P_g$ to variation in $Q$ (Figures 6a and 6c). At low $Q$, simulated photosynthetic $Q$ response of both the canopies was almost a straight line, indicating that $Q$ was the major limiting factor for $P_g$ up to a $Q$ of about 200 mol m$^{-2}$ s$^{-1}$. Beyond this value, $P_g$ increased by a factor of variable that was quite consistent to $Q$. The upper boundary of the distribution seemed quite well defined up to 500 mol m$^{-2}$ s$^{-1}$ but became more enhanced with further increases in $Q$. Arrows in Figures 6a and 6c highlight $Q$ values above, which simulated $P_g$ was saturated. Combined responses to $T_a$, $D$ and $f_b$ reduced $P_g$ at high $Q$.

The principal distribution pattern of $P_g$ in relation to $Q$ for the Solling data was similar to that for the Griffin data (cf. Figures 6a and 6c). However, the initial slope of the simulated canopy response function of the Solling canopy was less steep than for the Griffin canopy (0.041 instead of 0.058 mol CO$_2$ mol$^{-1}$ photons for $Q \leq 100$ mol m$^{-2}$ s$^{-1}$). The ratio of simulated initial slopes between the two sites was 0.67, whereas the quantum yields at the needle scale that were used in both simulations differed by only 6%. Therefore, we deduced that there is a canopy structural effect on PAR-use efficiency at the canopy scale and have used the model to show this effect.

The simulation revealed that the Solling canopy absorbed only 67% of incoming $Q$ whereas the canopy of the Griffin Forest absorbed 89% of incoming $Q$, i.e., the relative absorptance of the Solling canopy was only 75% of that of the Griffin canopy. There were larger gaps between the crowns of the trees in the Solling stand, whereas there were virtually no gaps between the crowns in the Griffin stand (cf. Figures 1a and 1b), and as a result some PAR passed directly through the gaps between crowns in the Solling canopy without interception, or was reflected through the canopy gaps to the ground or back to the atmosphere.

Nevertheless, if simulated $P_g$ is related to $Q_w$, the initial slopes of the $P_g(Q_w)$ functions are 0.061 and 0.066 mol CO$_2$ mol$^{-1}$ absorbed PAR for Solling and Griffin, respectively. The ratio of these true quantum yields of CO$_2$ uptake at the canopy scale is 93%, almost identical with the ratio of $\alpha_w$ at the needle scales that were used for Norway and Sitka spruce in the simulations. Thus, different needle physiology accounted for only 7% of the difference and the different absorptances of the two canopies contributed with 23% to the difference in apparent quantum yields between the two canopies.

Beyond the effects of 3D canopy structure, the higher $f_b$ at the Solling site may have contributed to the smaller PAR-use efficiencies, because beam radiation is less efficiently used for photosynthesis than diffuse radiation. To quantify this effect, we repeated the simulations with exchanged meteorological input. In both cases the Scottish maritime climate increased PAR-use efficiency by 13–14%. Given the same meteorological input, PAR-use efficiency of the younger Sitka spruce plantation was still 1.23 or 1.22 times as high as that of the mature Norway spruce stand. The differences in 3D canopy structure seem, therefore, to be one of the main reasons for the smaller mean $P_g$ of the Solling stand compared with the Griffin stand, despite higher $Q$ at the Solling site (see Table 3).

These findings are of particular importance for the simulation of $P_g$ with simplifying models, such as biogeochemical modules of general circulation models. Many of these models use the so-called light-use efficiency approach (Ruiny et al. 1999). Despite comparable LAI, needle physiology and soil water availability, PAR-use efficiencies differed greatly at the Solling and Griffin stands (0.023 versus 0.032 mol CO$_2$ per mol photon).

Discussion

What can be gained from intercomparison of simulated versus observed $P_g$?

Learning from a model application  Most of the model parameters were taken from the literature, with only a few derived from field measurements at the two forest sites. It was difficult to describe the dependence of electron transport rates on $Q_w$ at the single needle scale based on data from the literature. Much attention has focused on the biochemical key parameters of photosynthesis, $V_{\text{max}}$ and $J_{\text{max}}$ (Wullschleger 1993, Medlyn et al. 1999), but large uncertainty still exists about the values of the other parameters, the (true) quantum yield and the shape parameter ($\theta$) to describe photosynthetic electron transport in conifer needles. Unfortunately, simulation of photosynthesis in a dense canopy is highly sensitive to the quantum yield of electron transport. The two estimates we derived were similar to one another, but smaller than those published for a range of broad-leaved C$_3$ plants. An indication of the resulting limitation is evident in the analysis of residuals showing that, in both forest stands, there is an apparent drop in observed $P_g$ at high $D$, $Q$ and air temperature that was not reproduced by the model, but the model was appropriately sensitive to temperature and beam fraction.

Similarities between simulated and observed data  The two methods of obtaining independent estimates of $P_g$ are based on independent theories and technologies—eddy correlation and modeling. The comparison therefore enables detection of pos-
sible conflict between the estimates and thus, potentially, between the underlying theories. Given the complex character of the theories involved, an accidental match of the two flux estimates is unlikely, and even more so if achieved at two research sites simultaneously. If matching, the estimates can be carefully and optimistically interpreted as realistic and the comparison can serve as confirmation of the current state of knowledge.

**Differences between simulated and observed data** We demonstrated a general fit between model output and observation but the remaining differences between modeled and observed estimates should be further analyzed statistically to determine whether they are systematic or random. By using analysis of residuals, meteorological conditions can be identified, under which systematic discrepancies occur, thereby giving rise to new hypotheses about weaknesses and strengths of the two approaches.

At both sites, sensitivity of $P_g$ to high $D$ was apparent in the observed data but was not reflected fully by the MAESTRA simulation. Possibly this was an effect of the overestimation of canopy stomatal conductance by the model. In the version of MAESTRA used, feedback between stomatal conductance and soil water content was omitted, so that trees suffering from limited soil water availability could not be simulated realistically in the model. Although more than one earlier version of MAESTRO has included this feedback, leaf water potential has generally been found to be less important as a driver of stomatal conductance than $Q$ and $D$ for Sitka spruce in the Atlantic maritime climate of the British Isles, but this is less likely to be the case in the more continental climate of Central Europe at Solling. There the observed sensitivity of $P_g$ to $D$, together with the systematically lower observed than simulated $P_g$ during the early afternoon hours, may indicate that, even with apparently sufficient soil water availability, as assumed here for both sites, a link between CO$_2$ uptake and transpiration may exist. Baldocchi and Meyers (1998), for example, listed several physiological and morphological reasons for the increase in hydraulic limitation both of stomatal conductance and photosynthesis with increasing size and age of conifers. This trend is also indicated by our comparative study: the observed effects of $D$ on photosynthesis were larger in the older, taller Norway spruce stand than in the younger, shorter Sitka spruce stand.

Comparison of the two approaches not only revealed information on the model structure and parameters, but also on the nature of the turbulent fluxes and their ability to serve as test data for models. One difficulty is that a direct comparison of simulated canopy CO$_2$ gas exchange with measured turbulent CO$_2$ fluxes is impossible. Uncertainty is introduced to the observed $P_g$ estimate because of the difficulty of estimating total ecosystem respiration. In addition, turbulent flux data have an inherently large scatter that often does not reflect the dynamic behavior of the biological sinks and sources below the sensors, but instead reflects the large variability of turbulent transport processes in the atmospheric boundary layer. Thus, we do not expect MAESTRA to represent the highly variable turbulent flux data but rather the emerging main characteristics of the behavior of the system, which we take to be represented by the averaged turbulent fluxes.

**Sensitivity analyses** We evaluated the general match of the two estimates by regression analysis, by comparison of the ensemble averages and by the integral of the flux estimates over a longer period. An additional test that would directly lead to model or empirical data falsification would be to test the statistical significance of the differences between the two estimates, as suggested by Loehle (1997). However, for such an analysis, confidence intervals around the simulation results would need to be calculated and this was not attempted. This calculation would involve elaborate theoretical analyses of error propagation or advanced and statistical analyses, for example, the Monte Carlo simulation technique, and this has not yet been done with a complex model such as MAESTRA. The merit of such intensive model analyses would be to understand the model better and hence the simulated processes themselves.

Our sensitivity analyses of selected model parameters revealed two model (and system) properties: (1) the model has different sensitivities to the investigated parameters; and (2) the final simulation result, i.e., a time series of $P_g$ that is similar to the observed time series of $P_g$, can be achieved with many different parameter combinations. From these observations, the following conclusions about the value and the restrictions of intercomparison of simulated $P_g$ versus observed $P_g$ can be drawn.

(1) The model MAESTRA is over-parameterized for CO$_2$ fluxes at the canopy scale. Thus, a comparison with turbulent CO$_2$ flux data has the power to test only whether the model produced realistic simulated $P_g$, not how the model produced these results. This limitation has also been discussed by Falge et al. (2003), who considered the postulate that their model may have produced realistic results but possibly for the wrong reasons. Generally, it is the aim of science to find and use the simplest necessary formulation to describe a process in nature with a model (i.e., to conform to Occam’s razor), and a simple empirical model with only a few parameters is in fact able to describe the response of $P_g$ to environmental stresses (Goulden et al. 1996b, Jarvis et al. 1997, Aubinet et al. 2001, Pilegaard et al. 2001). But despite this, over-parameterization may not be interpreted in terms of redundancy of parameters, because a larger number of parameters is necessary to construct the CO$_2$ fluxes at the canopy scale from biological processes at smaller scales with measurable parameters. Thus to determine if a model uses the correct process descriptions and parameter values, we would need more information than canopy scale fluxes contain, including information about the spatial and temporal variability of photosynthetic rates at the shoot, branch and tree scales.

(2) The parameter set that has been used in a successful simulation has been tested as a whole, but the value of such a test for individual parameters is difficult to define. The test will have most significance for those parameters to which the simulation result is most sensitive and may well be of little or no relevance to other model parameters which may, nonetheless,
be of greater importance in other circumstances. Thus, a sensitivity analysis of the model output to a range of values of individual parameters and parameters in combination, covering a range of likely conditions, is a desirable next step.

(3) Model calibration by arbitrarily varying values of selected parameters for particular circumstances may lead to a better representation of the observed data by the model but will not overcome the problem of equifinality. The resulting parameter values have no better justification than those before calibration, and the model is transformed from an expression of the state of knowledge into a complex curve-fitting exercise.

In conclusion, we used simulations of canopy gross photosynthesis and turbulent flux measurements from two coniferous forests to discuss the challenges and potentials of an approach to process models that is oriented to learn from differences and from similarities with observed data, rather than to tune a model to fit the independent observed data. To keep model and test data independent we avoided model parameter calibration.

Comparison of gross photosynthetic rates simulated by the model MAESTRA with those calculated from measured turbulent net ecosystem CO$_2$ fluxes agreed within 10% for the two coniferous forests. Most of the residuals between the model simulation and the measured data were non-systematic; small systematic effects occurred only in situations with high $D_s$; an indication that the model failed to represent a possible feedback between plant water status, stomatal conductance and $P_g$, especially in the older and taller Norway spruce stand in Central Germany. The statistical noise in the observed turbulent flux measurements was inherent and did not reflect variability in the biological processes.

Observed $P_g$ of the two forest canopies differed by 25% and the model successfully captured this difference. The model simulations suggested that the smaller $P_g$ of the older, taller Norway spruce forest in central Germany was mainly caused by less canopy PAR absorption that was a consequence of gaps between the crowns and more clumped needle area distribution within the canopy, and the occurrence of larger beam fractions at that site compared with the younger, shorter and denser Sitka spruce plantation in Central Scotland.

The PAR-use efficiencies of gross photosynthesis differed by a factor of 1.4 between the two sites, despite similar leaf area, needle physiology and soil water status. Thus, the model simulations and field observations showed that the interaction between canopy structure and radiation regime must be considered in models that use PAR-use efficiency for prediction of daily canopy photosynthesis.

Sensitivity analyses of parameters that had been recalculated from other data sources revealed two important model and system properties. The sensitivity of the simulation of $P_g$ to certain model parameters was very different and the model was over-parameterized for $P_g$ at the canopy scale. Thus, the observed $P_g$ did not contain enough information to fully test the 3D model. Hence, it is not justified to interpret the comparisons of simulated and observed $P_g$ as measures of the validity of the model structure or individual model parameters. However, it was shown that the model structure and the parameters were not in conflict with the information from the turbulent flux measurements. Furthermore, the model structure was shown to be flexible enough to accommodate two very different forest canopies. Generally, it was shown that the model simulation in combination with the flux observations effectively contributed to understanding the magnitude of and the biophysical constraints on gross photosynthetic rates in mono-specific coniferous canopies. There is a scope to learn more about the nature and values of the model parameters and their relationships to other canopy traits such as age and development status from comparisons similar to this one.

Acknowledgments

This scientific collaboration was made possible through two Marie Curie Fellowships funded by the European Commission (EC, proposal Nos. ERB4001GT974186 and MEIF-CT-2005-008354). Long-term CO$_2$ fluxes and meteorological measurements have been funded by the EC as part of the EUROFLUX project (ENVCT 0095-0078) and by the German Federal Ministry of Education and Research BMBF (FKZ 0339474B, Sub-programme A7b). We are grateful for financial support and for the help of many technicians and research assistants and students who supported the investigations in the field and maintained the long-term measurements. Ingeborg Erler contributed to the gas exchange measurements at the Solling F1 site. Prof. Dr. Winfried Kurth provided three-dimensional leaf area distributions of the old spruce trees at the Solling F1 site. Dr. Dirk Gries supplied two gas exchange analysis systems.

References


**Appendix 1**

**Parameterization of leaf area distributions in MAESTRA**

The 3D-leaf area distribution is approximated in MAESTRA by two β-functions of the form:

\[
f(x) = ax^b(1-x)^c \quad \{x \in R, 0 < x < 1\}, \quad (A1)
\]

where \(x\) is a normalized length dimension and \(a, b\) and \(c\) are empirical parameters. In case of the vertical leaf area distribution (LAD), \(f_v(z')\), \(x\) is replaced by the normalized crown height, with \(H\) as the absolute crown height. For the radial distribution, \(f_a(r')\), the normalized local crown radius, \(r'\), is used; defined in the same manner as \(z'\) but using the local crown radius \(R(z')\). A third distribution may be the angular distribution function \(f_\theta(\beta')\). The rules for normalisation can be derived from Equations A2 and A3. Equation A2 describes the total leaf area of a tree (\(A_t\)) which is equal to the integral of LAD distribution function \(p_t\) over the three dimensions of space. A cylindrical co-ordinate system with azimuth angle \(\beta\) is used to define positions in the tree crown:

\[
A_t = \iiint_{0}^{2\pi} p_t(z, r, \beta) r \, dz \, dr \, d\beta \quad (A2)
\]

The leaf area distribution is normalized to integral 1 as defined in Equation A3:

\[
1 = \iiint_{0}^{1} f_v(z') f_a(r') f_\theta(\beta') \, dz' \, dr' \, d\beta' \quad (A3)
\]

Assuming azimuthal homogeneity, Equations A1 and A2 can be reduced to:

\[
A_t = 2\pi \iiint_{0}^{z} p_t(z, r) r \, dz \, dr \quad (A4)
\]

and

\[
1 = 2\pi \iiint_{0}^{1} f_v(z') f_a(r') \, dz' \, dr' \quad (A5)
\]

Equations A4 and A5 can be solved for the LAD distribution function to give:

\[
p_t(z, r) = \frac{A_t}{H R(z)^2} f_v(z') f_a(r') \quad (A6)
\]

The term multiplied by the two normalized relative LAD distribution functions is a scaling factor and is used to normalize the sampled leaf area densities. However, these derivations are still not complete because Equation A6 is fulfilled only if:

\[
1 = \int_{0}^{1} f_v(z') \, dz' \quad (A7)
\]

and consequently by substituting the vertical term in Equation A3 by Equation A7 gives:

\[
\frac{1}{2\pi} = \int_{0}^{1} f_a(r') \, dr' \quad (A8)
\]

MAESTRA offers three options to incorporate the leaf area distribution: (i) uniform, (ii) variable with height or (iii) variable both with height and with radius as has been described above. In the first case, \(p_t\) is a constant, defined as the total leaf area related to the total crown volume. In the second case the vertical LAD distribution function is described by \(f_v\), but \(f_a\) has the constant value of \(1/\pi\) in order to fulfill Equation A8, i.e., the \(\beta\)-function parameter \(a\) has the value \(1/\pi\) and \(b\) and \(c\) are null. In contrast, for the third case the integral of the normalized horizontal \(\beta\)-function is not a constant but depends on the relative distance of the maximum LAD distribution function from the stem to fulfill Equation A8. Only if the \(\beta\)-functions match these requirements will MAESTRA produce reason-
able results. The above approach was used to derive the parameters of the vertical and radial \( \beta \)-functions for the two forest stands in this study (see Table A1).

### Appendix 2

**Site parameters of forests other than Griffin and Solling F1 used for comparison**

**Fetteresso Forest** Sitka spruce, 27 miles south-east of Aberdeen, planted in 1948, mean tree height 11.5 m, 4100 trees ha\(^{-1}\), LAI 9.8, mean leaf area per tree 23.9 m\(^2\) at the age of 19 years (Norman and Jarvis 1974).

**Tummel Bridge** Sitka spruce, planted in 1968. Tree density before the investigation was 2500 trees ha\(^{-1}\), mean tree height was 10 m, mean leaf area per tree was 40.6 m\(^2\), LAI 10.1, at the age of 17 years (Wang 1988).

**Cloich** Is in Glentress Forest (55° 42' N 03° 16' W, 30 km south of Edinburgh) nine distinct agroforestry environments were created in 1985/1986 by thinning a commercially planted Sitka spruce plantation (2500 trees ha\(^{-1}\)). The low and intermediate stands were planted in 1972, the tall stand was planted in 1970. Twelve trees of each stand were harvested in 1986 for biometric investigation (Sinclair 1995).

### Appendix 3

**Parameters of leaf area distribution**

Table A1. Parameters of normalized \( \beta \)-functions of leaf area density distributions (see Appendix 1 and Figures 2 and 3) for spruce stands of different age and density (for data sources, see Appendix 2).

<table>
<thead>
<tr>
<th>Site</th>
<th>Vertical</th>
<th>Radial</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(ab)</td>
<td>(bc)</td>
</tr>
<tr>
<td>Griffin</td>
<td>36.79</td>
<td>0.95</td>
</tr>
<tr>
<td>Solling F1</td>
<td>12.47</td>
<td>1.67</td>
</tr>
<tr>
<td>Tummel</td>
<td>77.20</td>
<td>2.46</td>
</tr>
<tr>
<td>Fetteresso</td>
<td>(34.16 \times 10^4)</td>
<td>10.45</td>
</tr>
<tr>
<td>Cloich low</td>
<td>37.09</td>
<td>1.17</td>
</tr>
<tr>
<td>Cloich intermediate</td>
<td>37.09</td>
<td>1.17</td>
</tr>
<tr>
<td>Cloich tall</td>
<td>15.96</td>
<td>0.58</td>
</tr>
</tbody>
</table>

### Appendix 4

**Table A2. Physiological and biophysical parameters of the investigated Norway spruce and Sitka spruce stands.**

<table>
<thead>
<tr>
<th>Namelist</th>
<th>Parameter (names(^{12})) and units</th>
<th>Griffin</th>
<th>Solling F1 (^{8,11})</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSORB</td>
<td>Soil reflectance (RHOSOL) PAR(^{1}) NIR(^{2}) IR</td>
<td>0.1</td>
<td>0.30 0.05 0.1</td>
</tr>
<tr>
<td></td>
<td>Needle transitivity (ATAU) PAR(^{1}) NIR(^{2}) IR</td>
<td>0.03</td>
<td>0.26 0.0 0.03</td>
</tr>
<tr>
<td></td>
<td>Needle reflectance (ARHO) PAR(^{1}) NIR(^{2}) IR</td>
<td>0.09</td>
<td>0.33 0.05 0.07</td>
</tr>
<tr>
<td>JARGS</td>
<td>Cuticular conductance to CO(_2) (GSMIN) PAR(^{1}) NIR(^{2}) IR</td>
<td>0.003</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>Maximum stomatal conductance for CO(_2) (GSREF) PAR(^{1}) NIR(^{2}) IR</td>
<td>0.154</td>
<td>0.063</td>
</tr>
<tr>
<td></td>
<td>Minimum temperature (T0) °C PAR(^{1}) NIR(^{2}) IR</td>
<td>–5</td>
<td>–3</td>
</tr>
<tr>
<td></td>
<td>optimum temperature (TREF) °C PAR(^{1}) NIR(^{2}) IR</td>
<td>15</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Maximum temperature (TMAX) °C PAR(^{1}) NIR(^{2}) IR</td>
<td>40</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>D threshold at 50% reduction of stomatal conductance (D0) PAR(^{1}) NIR(^{2}) IR</td>
<td>375(^4)</td>
<td>4380</td>
</tr>
<tr>
<td></td>
<td>Sensitivity of stomatal conductance to external [CO(_2)] (GSJA) PAR(^{1}) NIR(^{2}) IR</td>
<td>0.0004(^3)</td>
<td>0.0004(^3)</td>
</tr>
<tr>
<td></td>
<td>NSIDES PAR(^{1}) NIR(^{2}) IR</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Leaf width (WLEAF) m PAR(^{1}) NIR(^{2}) IR</td>
<td>0.002</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Parameter of the hyperbolic response to Q (PAR0) PAR(^{1}) NIR(^{2}) IR</td>
<td>20(^5)</td>
<td>21.3</td>
</tr>
</tbody>
</table>

1 Wang (1988); 2 Norman and Jarvis (1974); 3 Barton (1997); 4 Sandford and Jarvis (1986); 5 Jarvis (1976); Continued overleaf
Table A2 Cont'd. Physiological and biophysical parameters of the investigated Norway spruce and Sitka spruce stands.

<table>
<thead>
<tr>
<th>Namelist</th>
<th>Parameter (names) and units</th>
<th>Griffin</th>
<th>Solling F1 (^8)(^{11})</th>
</tr>
</thead>
<tbody>
<tr>
<td>NPOL</td>
<td>Foliar nitrogen concentration g N m(^{-1})</td>
<td>2.2; 2.2; 2.0; 1.9(^5)</td>
<td>2.6; 1.6; 1.6; 1.7</td>
</tr>
<tr>
<td>JMAX-PARS</td>
<td>Convexity parameter of the (Q) response of (J) (THETA) dimensionless</td>
<td>0.8 (assumed)</td>
<td>0.8 (assumed)</td>
</tr>
<tr>
<td></td>
<td>activation energy temperature response of (J_{max}) (EAVJ) J mol(^{-1})</td>
<td>40000</td>
<td>40000</td>
</tr>
<tr>
<td></td>
<td>Deactivation energy temperature response of (J_{max}) (EDVJ) J mol(^{-1})</td>
<td>220000(^9)</td>
<td>220000(^9)</td>
</tr>
<tr>
<td></td>
<td>Entropy term in temperature response of (J_{max}) (DELSJ) J K(^{-1}) mol(^{-1})</td>
<td>710(^{10})</td>
<td>710(^{10})</td>
</tr>
<tr>
<td></td>
<td>Quantum yield of electron transport (AJQ) mol e(^{-}) mol(^{-1}) absorbed PAR</td>
<td>0.32</td>
<td>0.30</td>
</tr>
<tr>
<td>VCMAX-PARS</td>
<td>activation energy temperature response of (V_{max}) (EAVC) J mol(^{-1})</td>
<td>56000 (assumed)</td>
<td>56000</td>
</tr>
<tr>
<td>RDN</td>
<td>Slope of the linear dark respiration response to leaf nitrogen content (RDA) (\mu)mol g(^{-1}) s(^{-1})</td>
<td>0.87(^7)</td>
<td>0.80</td>
</tr>
<tr>
<td></td>
<td>Offset of the linear dark respiration response to leaf nitrogen content (RDB) (\mu)mol m(^{-2}) s(^{-1})</td>
<td>(-0.71)^7</td>
<td>0.56</td>
</tr>
<tr>
<td>RDPARS</td>
<td>Reference temperature for respiration response to temperature (RTEMP) °C</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Scaling constant in the exponential respiration response function to temperature (Q(_{10F})) °C(^{-1})</td>
<td>0.083(^1)</td>
<td>0.131</td>
</tr>
<tr>
<td>SLA</td>
<td>Specific leaf area for each crown layer m(^2) kg(^{-1})</td>
<td>3.76; 3.38; 3.55; 3.80; 4.69(^6)</td>
<td>3.7; 6.1; 6.1; 5.7</td>
</tr>
</tbody>
</table>

\(^5\) Wingate, unpublished data; \(^7\) Meir et al. (2002); \(^8\) Olteev, Panferov and Ibrom unpublished data; \(^9\) Farquhar et al. (1980); \(^10\) fixed parameter; \(^11\) Knyazikhin et al. (1997); \(^12\) names for parameters and their parameter groups used in the MAESTRA documentation.