

Parametrization of two photosynthesis models at the canopy scale in a northern boreal Scots pine forest

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ABSTRACT

In this work, eddy covariance data from a northern boreal Scots pine (*Pinus sylvestris*) stand were used in the parametrization of two up-scaled leaf-level photosynthesis models. The parametrization was carried out by eddy covariance data inversion. The biochemically based Farquhar model parameters, the maximum rate of electron transport ($J_{\max}$) and maximum rate of carboxylation [$V_{c(\max)}$], were both obtained from the temperature responses measured by the eddy covariance. The semi-empirical model, based on optimizing water use and carbon gain, was parametrized according to the seasonal behaviour of the parameter β . The parametrization of the models was performed for the year 2001, while 2002 was used as a test year to study the models' capabilities. Both of the models tracked daily CO_2 assimilation fairly well, reaching the high growing-season rates in mid-June and starting the autumn drawdown at the beginning of September. The incapability of the models to track the diminishing of CO_2 fluxes during very dry days brings up the issue of combining a soil model into the canopy model. The biochemical model parameters have temperature responses that change during the growing season. The biochemical model responds more to the temperature, whereas the semi-empirical model is strongly driven by the light level.

1. Introduction

Canopy-scale forest models are important for the interpretation of measured gas exchange data and for predicting the behaviour of a forest stand in changing climatic conditions. Their performance can therefore be analysed by using eddy covariance data as an independent reference (Kellomäki and Wang, 2000; Ogée et al., 2003; Wang et al., 2003; Simon et al., 2005). There have been simple models that do not include the processes within the forests but instead approximate the light use efficiency of the canopy as means to evaluate the CO_2 exchange (Boote and Lommis, 1991; Dewar et al., 1998). Using leaf-level models and their scaling up to the canopy has provided better results but the parametrization of these models has proved to be difficult.

The leaf-level parametrization itself is not a straightforward task to perform in the detail required by the canopy level model. The different leaf-age classes act differently (Porté and Loustau, 1998) and also location of the forest (Medlyn et al., 2002a) and seasonality play a role (Wirtz, 2000; Wilson et al., 2001; Medlyn et al., 2002b).

Using scarce observations of leaf-level parameters in large scale models has been conducted even though it is not obvious that the non-linear scaling up procedures performed by the models is reliable and Wang et al. (2006) therefore recommend larger-scale estimations of the parameters.

We chose two different models and examined the possibilities of parametrizing these models using eddy covariance data. The first of the models was the well known and widely used mechanistic model developed by Farquhar et al. (1980); it will be referred to hereafter as the BM (Mechanistic Biochemical theory based photosynthesis and conductance model on leaf gas exchange) model. It describes the biochemical phenomena of the photosynthesis inside the leaf, and in its simplest form the CO_2 assimilation is limited either by the activity of Rubisco (ribulose 1,5-biphosphate carboxylase/oxygenase) or by the RuBP (ribulose 1,5-biphosphate) regeneration in the photosynthetic carbon reduction cycle. The model concentrates on the biochemistry and does not contain a formulation for the opening of the stomata; conductance is therefore taken from other models (Ball et al., 1987). The model formulation adopted is from de Pury and Farquhar (1997) and it has been used in Finland by Kellomäki and Wang (2000) and Juurola et al. (2005). The BM model parameters have previously been estimated on the canopy scale by inversion, for example, by Arneth et al. (1998) and Rayment

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et al. (2002). More sophisticated methods have been used in larger-scale parameter estimations (Knorr and Kattge, 2005).

The other model used is called the optimal stomatal regulation model, hereafter referred to as the OM (Optimization theory based environmental conditions limited photosynthesis and conductance model on leaf gas exchange) model. It is based on the optimization theory first introduced by Cowan (1977), according to which a plant opens its stomata so as to maximize the amount of CO₂ uptake while simultaneously minimizing transpiration. This idea has been used in the context of modelling conductance with the biochemical model (Williams et al., 1996) and in the interpretation of canopy-level measurement data (Lloyd et al., 2002). A CO₂ assimilation model has also been derived according to this principle (Hari et al., 1986; Mäkelä et al., 1996). It has been successfully applied at both the leaf (Berninger et al., 1996; Hari et al., 1999) and canopy levels (Hollinger et al., 1998; Mäkelä et al., 2006).

Our aim was to study the possibilities of the parametrization of two different leaf-level gas exchange models from eddy covariance data, by keeping the scaling up procedures simple. We also compared the obtained parameters to the leaf-level measurement results. Comparison between the models provided an answer whether the more empirical model (OM) yielded better results than the more sophisticated model (BM) and more careful examination showed what can be gained by using the BM model.

In this paper, we first describe our measurement site, and introduce the models and their up-scaling to the canopy level. The parametrization of the models is then carried out by inversion from the eddy covariance data, and the models' functionality at the measurement site is studied. The seasonal development and the temperature dependencies of the parameters found are also examined. The flux values obtained using the two models are compared to each other and to the measurement data at different time scales. Special attention is given to the challenging conditions at the beginning and the end of the growing season. Finally, the models are applied to another year's data, which have not been used in the inversion. This tests the predictive capabilities of the models.

2. Materials and methods

2.1. Site description

The measurement site was situated in Northern Finland at Sodankylä (67°21.712' N, 26°38.270' E, elevation 179 m a.s.l.), within the Finnish Meteorological Institute's Arctic Research Centre. The forest is a main site in the CARBOEUROPE flux network (www.carboeurope.org).

The forest was a Scots pine forest (*Pinus sylvestris*) with a total leaf area index (LAI) of 3.6 as determined from a forest inventory in early autumn. The needle area was determined by applying a regression model to tree data from 859 trees from 41

sampling areas which were located in eight equally separated (45°) directions around the micrometeorological mast. Tree data were recorded every 50 m distance increments from the mast. The regression model was based on destructive sampling (trunks, branches, whorls) of 10 trees of representative ages. Needle areas were determined from the dry masses after measuring needle dry masses and lengths of subsamples and applying a second order polynomial to relate needle length and area.

The forest had been naturally regenerated after forest fires. The stem density was 2100 ha⁻¹ and the dominant tree height was 12.7 m. The trees were approximately 100 years old. The sparse ground vegetation consisted of lichens (73%), mosses (12%) and ericaceous shrubs (15%). The stand was located on fluvial sandy podzol. The soil texture was 0.3/91.2/4.3/4.2% of sand, till, clay and stones, respectively. The yearly average (1961–1990) temperature and precipitation values were –1.0 °C and 499 mm, respectively. The ground is usually covered by snow from October until the middle of May, and the uppermost soil layers are frozen during the wintertime.

2.2. Micrometeorological measurements

The CO₂ flux was measured by the micrometeorological eddy covariance (EC) method. The 3-D sonic anemometer (SWS 211, Applied Technologies Inc., USA) was mounted at a height of 23 m in a tower, and the inlet tube of the closed path CO₂/H₂O analyser (LI-6262, LiCor Inc., USA) was within the anemometer. We used a sampling rate of 10 Hz. We used our EC data acquisition and calculation program, which makes coordinate rotation and data detrending by an autoregressive running-mean filter with a 200-s time constant, corrects the lag between the time series resulting from the transport through the inlet tube, and corrects high-frequency loss due to imperfect sensors. More details of the measurement system and data manipulations and corrections are to be found in Aurela (2005).

The CO₂ concentration was measured by a LI-6262 at a height of 23 m. Additional meteorological measurements were done at the site. Temperature and relative humidity were measured at 8 m (model HMP35C, Vaisala, Helsinki, Finland). Photosynthetically active radiation (PAR) was measured towards the sky and the ground at 48 m (model LI-190SZ, LiCor Inc., USA). The air pressure and hourly precipitation were obtained from an automatic weather station close to the observatory buildings located 300 m from the tower. Before June 16, 2001 the precipitation was obtained from the daily manual measurements conducted at the observatory.

2.3. Leaf chamber measurements

Needle respiration and the BM model parameters were determined by leaf chamber measurements made on Scots pine needles during July in 2002. The measuring apparatus was a LI-6400 (LiCor Inc., USA) used with a conifer chamber (model

LI-6400-05, LiCor Inc., USA). Measurements were made on four trees that were located in a well-illuminated environment. The measured branches were located in the lower part of the crown and the measurements were conducted on 1-year-old needles.

To determine the needle respiration, the shoot was first placed in the conifer chamber and the chamber stabilized for approximately 5 min. The humidity, CO₂ concentration and air temperature inside the chamber were kept approximately constant during the measurement. The chamber was then darkened and the respiration flux measured. The shoots were later cut from the trees and scanned with a scanner (CanoScan FB330, Canon, Japan); the leaf area of each shoot was determined from the projected area. In order to obtain the BM model parameters, light response curves and CO₂ concentration response curves were measured using a protocol given in the manual (LI-6400 Manual, LiCor Inc., 1999). The BM model parameters estimated from two leaf chamber measurements were only used in validation of the parameters obtained by inversion from the eddy covariance data.

2.4. The models

2.4.1. The BM model. The first leaf-level model we used was the BM model (Farquhar et al., 1980; de Pury and Farquhar, 1997). According to the model, CO₂ carboxylation can be limited in two different ways, depending on the CO₂ concentration and the irradiance. The RuBP regeneration-limited rate of net CO₂ exchange A_j restricts CO₂ carboxylation at high CO₂ concentrations and low radiation levels. The Rubisco activity-limited rate A_c restricts CO₂ carboxylation at low CO₂ concentrations and high light levels.

The net assimilation rate can therefore be expressed as the minimum of these two assimilation rates, which are:

$$A_j = J \frac{c_i - \Gamma_*}{4(c_i + 2\Gamma_*)} - R_d \quad (1)$$

and

$$A_c = V_{c(\max)} \frac{c_i - \Gamma_*}{k_c(1 + o/k_o) + c_i} - R_d. \quad (2)$$

In these equations $V_{c(\max)}$ is the maximum rate of carboxylation, J is the potential electron transport rate, R_d is the rate of non-photorespiratory respiration, k_c and k_o are the Michaelis-Menten constants for CO₂ and O₂, Γ_* is the CO₂ compensation point in the absence of non-photorespiratory respiration, o is the oxygen concentration in chloroplasts (assumed constant) and c_i is the carbon dioxide concentration inside chloroplasts. The potential electron transport rate is calculated as

$$J = \frac{qI_o + J_{\max} - \sqrt{(qI_o + J_{\max})^2 - 4\Theta qI_o J_{\max}}}{2\Theta}, \quad (3)$$

where I_o is a function of the incident irradiance, $J_{\max}$ is the maximum rate of electron transport, Θ is the convexity of the light

response curve and the light use efficiency factor is q . The symbols and their units are given in Table 1.

The temperature dependence of Γ_* was taken from Brooks and Farquhar (1985) and the temperature dependencies of the Michaelis-Menten constants were adopted from Farquhar et al. (1980) and Harley and Baldocchi (1995). The values for the light use efficiency factor q and the convexity of the light response curve Θ were taken from leaf chamber data obtained in Värriö, a Scots pine site that is located at the same latitude as Sodankylä (Aalto, 1998). Often the light use efficiency is estimated in models by inversion (Wang et al., 2003, Verbeeck et al., 2006). However, in the study by Rayment et al. (2002), no seasonality in light use efficiency was observed at the canopy level. We studied the effect of the light use efficiency in modelling results and the shape of the light relationship of the CO₂ fluxes of the models and the measurements.

The magnitudes and temperature dependencies for $V_{c(\max)}$ and $J_{\max}$ will be estimated from the eddy covariance data. An Arrhenius-type temperature dependency was assumed for the two parameters, as represented by Harley and Baldocchi (1995):

$$f_T = f_0 \exp \left[\frac{E_f(T - 298.15)}{298.15RT} \right], \quad (4)$$

where f_0 denotes the parameter, E_f is the activation energy, R is the gas constant and T is temperature (K).

The Farquhar model does not contain stomatal conductance. The very commonly applied Ball-Berry conductance formulation was used in conjunction with the Farquhar model. The conductance g_{BB} is described as

$$g_{BB} = g_0 + g_1 \frac{RH \times A_f}{c_a}, \quad (5)$$

where RH is the relative humidity, A_f is the assimilation rate, c_a is the ambient CO₂ concentration and g_0 and g_1 are empirical constants. The empirical constants were approximated using eddy covariance and leaf chamber data measured at the Sodankylä Scots pine site; these are given in Table 1.

2.4.2. The OM model. The formulation used for the OM model was adopted from Hari and Mäkelä (2003) and Kolari et al. (2007). The CO₂ assimilation A is represented by

$$A(t) = \frac{[g(t)C_a + r]f[I(t)]}{g(t) + f[I(t)]}, \quad (6)$$

where C_a is the ambient CO₂ concentration, r is the respiration rate and g is the conductance.

The function f of irradiance (I) shows the saturation of the biochemical reactions, and is given by

$$f(I) = \frac{\beta I}{I + \gamma}, \quad (7)$$

where γ represents the function's saturation value and β is a parameter describing the photosynthetic efficiency.

Table 1. The definitions and values of the parameters used in the BM and OM models

Definition	Symbol and units	Value
The BM model		
Rubisco-limited rate of assimilation	A_c ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	
RuBP-regeneration limited rate of assimilation	A_j ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	
CO ₂ concentration in intercellular spaces	c_i ($\mu\text{mol mol}^{-1}$)	
Potential rate of electron transport	J ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	
Maximum rate of electron transport	J_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	
CO ₂ compensation point in the absence of non-photorespiratory respiration	$\Gamma_{*,298}$ ($\mu\text{mol mol}^{-1}$)	44.7 ^a
Non-photorespiratory respiration	R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	See Appendix B
Maximum rate of carboxylation	$V_{c(\text{max})}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	
Michaelis–Menten constant for CO ₂	$k_{c,298}$ ($\mu\text{mol mol}^{-1}$)	275 ^b
Michaelis–Menten constant for O ₂	$k_{o,298}$ ($\mu\text{mol mol}^{-1}$)	420 000 ^b
O ₂ concentration in intercellular spaces	o ($\mu\text{mol mol}^{-1}$)	210 000
Incident radiance	I_0 ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	
Effectivity factor for the use of light	q ($\text{mol e}^-/\text{mol quanta}$)	0.14 ^c
Convexity factor of the light response curve	Θ	0.70 ^c
CO ₂ assimilation rate	A_f ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	
Stomatal conductance	g_{BB} ($\text{mol m}^{-2} \text{s}^{-1}$)	
Minimum stomatal conductance to H ₂ O	g_0 ($\text{mol m}^{-2} \text{s}^{-1}$)	0.01 ^d
Empirical coefficient representing the composite sensitivity of conductance to A	g_1 ($\text{mol m}^{-2} \text{s}^{-1}$)	5.0 ^d
Relative humidity	RH	
CO ₂ concentration in ambient air	c_a ($\mu\text{mol mol}^{-1}$)	
The OM model		
CO ₂ assimilation rate	A ($\text{mol m}^{-2} \text{s}^{-1}$)	
Stomatal conductance	g (m s^{-1})	
CO ₂ concentration in ambient air	C_a (mol m^{-3})	
Respiration rate	r ($\text{mol m}^{-2} \text{s}^{-1}$)	See Appendix B
Saturation deficit of water vapour	D (mol m^{-3})	
Ratio of H ₂ O to CO ₂ diffusion rates	a	1.6
Photosynthetic capacity	β (m s^{-1})	
Saturation value of the light response curve	γ (m s^{-1})	(1000 ^e)
Water-use efficiency	λ [mol CO_2 ($\text{mol H}_2\text{O}$) ⁻¹]	0.0041 ^e

^aBrooks and Farquhar (1985).^bHarley and Baldocchi (1995).^cAalto (1998).^dEstimated from Sodankylä measurements.^eEstimated from Värriö leaf chamber measurements.

The conductance g is included in the model and is formulated as

$$g = \left(\sqrt{\frac{C_a - \{r/f[I(t)]\}}{\lambda a D(t)}} - 1 \right) f[I(t)], \quad (8)$$

where λ is the cost of transpiration, D is the saturation deficit of water vapour and a is the ratio of the diffusivity of water vapour to that of CO₂. The units of the symbols are shown in Table 1.

The parameters λ and γ were assumed to remain constant during the growing season and they were adopted from the leaf chamber measurements in Värriö, described in Hari and Mäkelä (2003). The β parameter will be determined from the eddy covariance data.

These two models have been compared at the leaf level by Aalto et al. (2002) using leaf chamber data from Värriö.

2.5. The up-scaling and inversion of the models

The leaf-level models needed to be scaled up to the canopy level. Tree biomass data was used to construct a vertical profile of biomass distribution for a pine tree using the beta distribution (Wu et al., 2003). We used a multilayer approach and divided this vertical profile into four parts, each of which had about a quarter of the total leaf area.

Using these four layers, the radiative transfer into the canopy was calculated, employing the two-stream approximation radiative transfer model developed by Sellers (1985). In the model

the direct radiation is approximated by Beer's law, while diffuse radiation is directed upwards and downwards inside the canopy. The nature of the diffuse radiation is dependent on the amount of direct radiation in the total radiation. The potential PAR was calculated as in Savijärvi (1990), and the parameters of the radiative transfer model, that are described in Appendix A.1., were taken from Knorr (1997).

When scaling the BM model parameters $J_{\max}$ and $V_{c(\max)}$ in multiple layers, they were assumed to decrease proportionally to the percentual PAR (Kull and Jarvis, 1995; Sellers et al., 1992). A separation was made into sunlit and shaded leaves (Thornley, 2002) in distinct layers during the computation of the BM model. The equations are displayed in Appendix A.1.

Respiration was divided into soil and foliar respiration, and was fitted using the eddy covariance and leaf chamber data. Stem respiration measurements for Finnish Scots pine have been made in mid-Finland (Zha et al., 2004) and these results were first also used in modelling of respiration. However, because Sodankylä forest has large increase in the level of respiration at the latter part of the summer it was difficult to apply a full respiration model to the site. Therefore, a simple approach was chosen and bi-weekly changing fittings to the experimental data were used instead. The temperature relationship used for the respirations, as well as the fitted respiration values for the foliar respiration, are given in Appendix B.1.

In the year 2001, in order to ensure successful inversion, the measured CO_2 flux values used were highly selected from the available data. No fluxes during rainy periods were used. The wind directions from 270° to 340° do not represent a typical source area, and so these data points were also removed from the analysis. In 2002, less stringent conditions were used in data selection regarding to stationary and turbulence conditions (Carboeurope class 1). The time period under investigation started from the end of April, when the CO_2 fluxes first appeared, and lasted until the end of September, when the photosynthetic activity ceased.

The most important site- and species-dependent parameters of the BM model [$J_{\max}$ and $V_{c(\max)}$] and the OM model (β) were inverted from the half-hourly flux measurements. During the inversion the BM model was run in four layers where the parameters were scaled as described earlier. In order to achieve temperature responses for the BM model parameters it was necessary to attempt many different methods and the scaling up procedures were improved simultaneously. The influence that the light use efficiency q probably had with the parameters was also investigated by performing the inversions with the value of q both doubled and halved.

The time periods for different fits for the BM parameters were decided after testing out various time periods and fits. The decision was made according to how the temperature responses of the parameters varied according to season. There appeared to be certain break points but the deciding the time periods was also based on the performance of the model.

The parameters were estimated from the data for the year 2001, while the model performance was checked using independent data from 2002. The performance of the models was examined by calculating r^2 and root mean square error (RMSE) values. These equations are shown in Appendix C. The model was also run by parameter values taken from literature (Wang et al., 1996) and with the parameters from the leaf chamber measurements with temperature responses adapted from literature (Aalto, 1998). In addition, it was also examined what kind of results were obtained by combining the BM model photosynthesis part with the OM model's conductance and how the effect of drought could be implemented to the model. In order to have a closer look in the drought effect a coefficient was introduced to the BM model. It multiplied the second term on the right hand side in the Ball-Berry conductance function in eq. 5. The coefficient g_D was a sigmoid function which decreased as a function of increasing VPD.

All the calculations were performed using Matlab 7.0. For the minimizing functions of one variable, the packages used in the fitting procedures applied the golden section search and the parabolic interpolation algorithm. The square of the remainder of the difference between measured and modelled values (the residual) was minimized. In the minimizing of the functions of several variables, the fitting procedures employed the Nelder-Mead simplex search algorithm (Lagarias et al., 1998). The factor to be minimized here was the square of the norm (largest singular value) of the error matrix. The error matrix was the residual of the measurement.

2.6. Inversion of the BM model

The temperature dependency of $J_{\max}$ was estimated from the flux measurements below the change point in the $J_{\max}/V_{c(\max)}$ -limited rates, as suggested by Lloyd et al. (1995). All the half-hourly measurements between 10 and 12 a.m. that had a measured PAR between 600 and 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ were included. The lower light level was chosen to minimize the limitation by the light use efficiency q in the canopy CO_2 assimilation rate. The upper limit was below the change point in the $J_{\max}/V_{c(\max)}$ -limited rates, defined from the light relationship curves measured by eddy covariance. The data points from the afternoon were excluded because of large VPD:s and possible drought effects. In the dataset selected according to these criteria, all canopy layers were $J_{\max}$ -limited, and thus $J_{\max}$ could be easily solved from the half-hourly flux measurements. The well-known Arrhenius-type curve was fitted to the $J_{\max}$ -temperature relationship.

At high irradiance levels, the upper layers of the canopy were limited by $V_{c(\max)}$ while the lower, shaded layers were limited by $J_{\max}$. This colimitation was reflected in the flux values, since all the layers were summed up together to obtain the total canopy flux. Thus, when $V_{c(\max)}$ was solved from the total canopy flux measurements, the result was dependent on the earlier fit for $J_{\max}$. However, the $J_{\max}$ -limited layers contributed less than

30 percent of the total flux in saturating light conditions, and $V_{c(max)}$ was thereby dominant in the conditions when $V_{c(max)}$ was calculated. When $V_{c(max)}$ was determined using data points measured also between 10 and 12 a.m. where the light level was above $800 \mu\text{mol m}^{-2} \text{s}^{-1}$, then the fitted curve for J_{max} was also used. An Arrhenius-type dependency was used for $V_{c(max)}$ and temperature.

2.7. Inversion of the OM model and other estimation methods

For the OM model, the parameter β (eq. 7) was determined by model inversion from the data for the year 2001. The daily values for β were calculated as an average of the best-quality data point values between 10 and 12 a.m., obtained from the inversion of the flux measurements. The seasonal behaviour of β was approximated by a third-order polynomial, which was fitted to the points and was used to drive the model. The fitting period for β started on May 1, as this was the day when the spring recovery of the forest started according to Suni et al. (2003). The same polynomial fit was used for β in 2002.

On the other hand, β may be expressed as a function of time together with seasonal temperature changes, taking into account the ontogenetic development of the photosynthetic activity (Pelkonen and Hari, 1980; Mäkelä et al., 2004). This so-called state of acclimation (S) was calculated as described in Mäkelä et al. (2004) and was scaled to the same level as the β obtained by inversion. S is based on an averaging of the air temperature. Another way to assess the seasonal development of β is to estimate it from leaf chamber measurements. The leaf chamber measurements used were performed in Värriö and are described in detail in Kolari et al. (2007). The obtained value for β was again scaled to the level of the inversed β . Both ways of estimating the parameter β were studied by investigating the model's performance with these parameter values for the year 2001.

3. Results

3.1. J_{max} and $V_{c(max)}$ and in the BM model

The temperature dependency of the J_{max} values is shown in Fig. 1. These points were from the morning period, from 10 to 12 a.m. and were all used in the fitting of the parameter. According to the May values, J_{max} did not show a clear increase with temperature. In June larger values were obtained at higher temperatures, but the scattering was considerable. Values smaller than 30 and larger than $70 \mu\text{mol m}^{-2} \text{s}^{-1}$ were present at temperatures over 15°C . In July there were not many points, and in August the scattering was also large, with two large values also occurring at lower temperatures. In September, the increase of J_{max} with temperature was obvious, but it remained at a higher level at lower temperatures than in May, showing the need for a second separate fit for the parameter J_{max} . The time period for

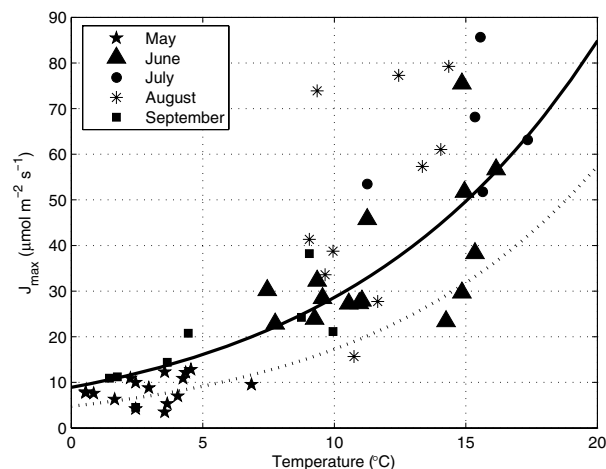


Fig. 1. The temperature response of the values of the parameter J_{max} obtained by inversion of half-hourly values. The exponential fit for the spring period (May 1–June 3) is shown with the dashed line, while the fit applied for the rest of the growing season is the solid one.

the first fit was from the beginning of May to June 3. The couple of lower points located around 15°C occurred in very early June and therefore June 3 was set as a time limit. A second fit was done for the rest of the growing season (June 4–September 31). The constant f_0 and the activation energy obtained from the fits are presented in Table 2.

The inversed values of parameter $V_{c(max)}$ also had a clear temperature response, as can be seen in Fig. 2. As in the case of J_{max} , $V_{c(max)}$ values showed only a weak temperature relationship in May, while the larger scatter occurred in June. In July and August all parameter values were found at medium to high temperatures. In September the points were located above the spring values in the low temperature range. After experimenting with different time periods, it was concluded that three separate fits produce the best results for the year 2001. The spring period lasted from May 1 to June 3, while the second fit consisted of the time period from June 4 to June 27 (early summer). The third fit was made to the late summer (June 28–September 31). The fitting parameters are displayed in Table 2. Overall, the inverted parameter values showed a clear response to temperature and it was a straightforward matter to make the fits.

Temperatures did not usually reach the highest summer values during the time periods selected for fitting, since the afternoons were rejected. Furthermore, applying the fitted, exponentially increasing function straightforwardly to the high temperatures did not seem to produce very good results. For running the model, maximum values for the two parameters were set for high temperatures. J_{max} was set to a constant $55 \mu\text{mol m}^{-2} \text{s}^{-1}$, the value when the fitting curve reached a level of 20°C in spring; in summer the value was $85 \mu\text{mol m}^{-2} \text{s}^{-1}$. In the case of $V_{c(max)}$, for temperatures of 20°C and upwards its value was estimated to be

Table 2. The parameters obtained from the temperature fits for the BM model parameters

Definition	Symbol and unit	For	Value
Activation energy for CO ₂ and light saturated assimilation	E_f (J mol ⁻¹)	$J_{\max}$ (1 May–3 June)	82 928
		$J_{\max}$ (4 June–31 September)	75 031
		$V_{c(\max)}$ (1 May–3 June)	75 477
		$V_{c(\max)}$ (4–27 June)	86 446
		$V_{c(\max)}$ (28 June–31 September)	84 152
Constant	f_0	$J_{\max}$ (1 May–3 June)	101
		$J_{\max}$ (4 June–31 September)	142
		$V_{c(\max)}$ (1 May–3 June)	13.9
		$V_{c(\max)}$ (4–27 June)	23.6
		$V_{c(\max)}$ (28 June–31 September)	40.3

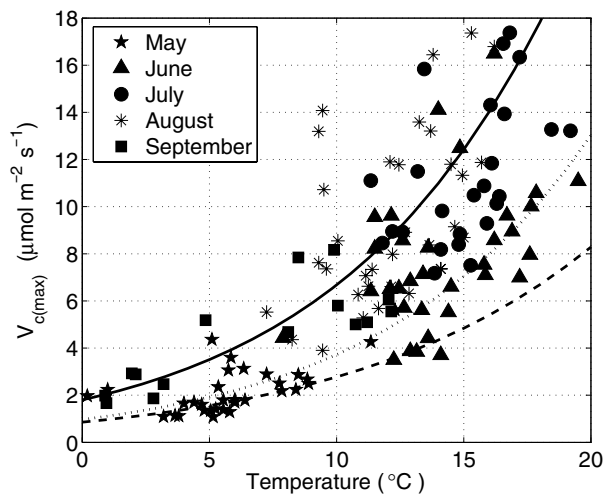


Fig. 2. The temperature response of the value of the parameter $V_{c(\max)}$ gained by inversion of half-hourly values from 10 to 12 a.m. The exponential fit for the spring time (May 1–June 3) is the dashed line, the early summer fit (June 4–June 27) is the dotted line and for the late summer the exponential fit is shown by the solid line.

8, 13 and 23 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during spring, early summer and the late summer, respectively.

3.2. β in the OM model

The β values produced by the various different methods for year 2001 are shown in Fig. 3. The scattered points are values gained by inversion, while the polynomial fit that was used to drive the model is the solid line. The β estimated from chamber measurements in Värriö and the temperature development by the state of acclimation are also shown.

Inversed values of β appeared to be quite scattered. The polynomial fit was unable to fully mirror the variation in the parameter values. For example, β values were lowered at the end of May due to night frosts. The decrease was seen both in the estimates from chamber measurements and from the state of acclimation, but a simple polynomial fit was too coarse to model

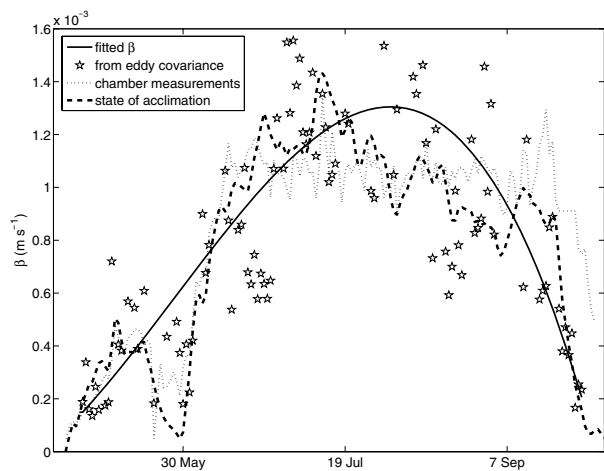


Fig. 3. The scattered points represent the inversed values for β and the solid line is the fitted polynomial. The dotted line shows the scaled β estimated from chamber measurements and the dashed line displays the scaled state of acclimation.

this. However, the inversed parameter did not seem to have a clear temperature dependency at the canopy level, and therefore a temperature relationship could not be applied as with the BM approach. A lowering in β occurred also in mid-June and at the end of August; the polynomial fit missed this behaviour too, as did the estimates from chamber measurements and the state of acclimation. The chamber measurements exaggerated β during September.

In Fig. 3 the inversed values of the parameter β result in the optimum behaviour of the model. The parameter estimated from chamber measurements showed the weakest performance. The polynomial fit and state of acclimation both appeared to give equally good estimates of the parameter β .

3.3. Model runs for the years 2001 and 2002

3.3.1. Correlations with measurements. The results from the model runs versus the measurements for the half-hourly CO₂

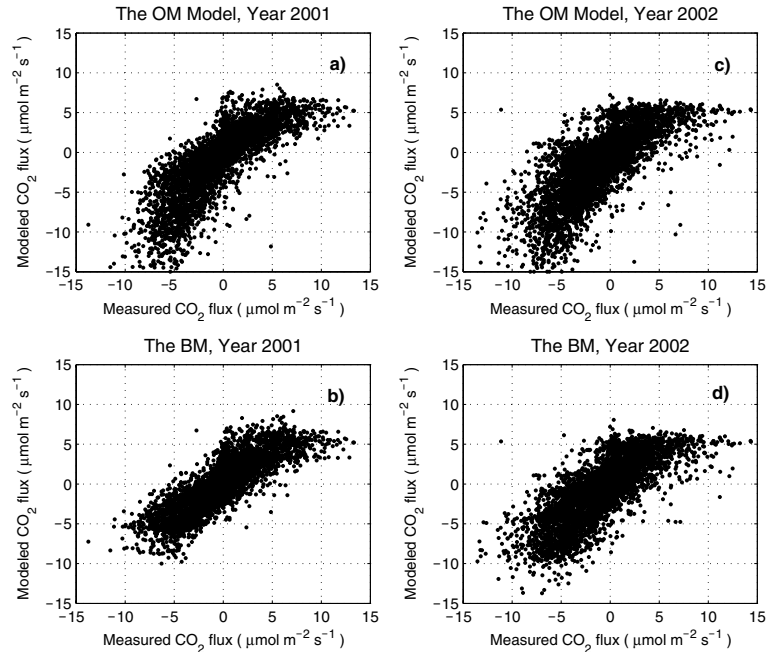


Fig. 4. The half-hourly measured CO₂ fluxes versus the modelled fluxes for the years 2001 and 2002, calculated by the OM model (a and c) and the BM model (b and d).

Table 3. The r^2 and RMSE values of the models separately for half-hourly and averaged daily values for years 2001 and 2002

Half-hourly values				
Year	The BM model		The OM model	
	r^2	RMSE	r^2	RMSE
2001	0.71	1.85	0.66	2.39
2002	0.58	2.50	0.56	2.86
Averaged daily values				
Year	The BM model		The OM model	
	r^2	RMSE	r^2	RMSE
2001	0.76	0.91	0.71	1.35
2002	0.71	1.13	0.68	1.47

fluxes are shown in Fig. 4 for 2001 and 2002 and for both of the models. The r^2 values and the RMSEs are displayed in Table 3. The r^2 values and the RMSEs were also computed for the daily average (Table 3).

In Fig. 4 the frequent overestimation of assimilation in the OM model was seen in both years. The BM model succeeded better in this respect. The largest respiration fluxes were not completely represented by the respiration fits. The r^2 values presented for the half-hourly values in Table 2 were evidently better for 2001, since it was used for the parametrization and a more refined data set was used. Compared to each other, the models gave similar r^2 , with the BM model reaching higher values. The RMSE values are slightly smaller for the BM model. The r^2 values for daily averages were at approximately the same level as the half-hourly r^2 values for 2001. The RMSE values were lower than for the

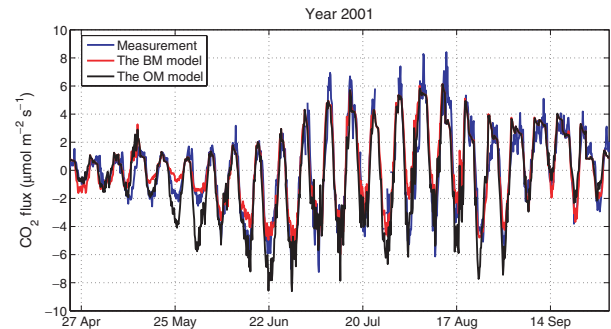


Fig. 5. The weekly averages for diurnal periods for the measurements and the models from the end of April till the end of September in 2001.

half-hourly values, and for the BM model performing slightly better.

3.3.2. Diurnal and seasonal responses of the models. To study the performance of the models on a diurnal and seasonal scale the weekly averages of the diurnal half-hourly values were taken; these are shown in Fig. 5 for the year 2001 and in Fig. 6 for 2002. In the figures, each point shown represents a seven-point mean for each half-hour over the daily cycle. Weeks, for which there was less than 1 d of observations or modelling results are not displayed.

The model results were nearly as good for both years, 2001 and 2002. The BM model performed well during the first three weeks in Fig. 5. The mismatching evening points during the third week were caused by one very warm night. However, during the last 2 weeks of May, the model did not reach the measured CO₂ fluxes because June night frosts greatly affected the parametrization.

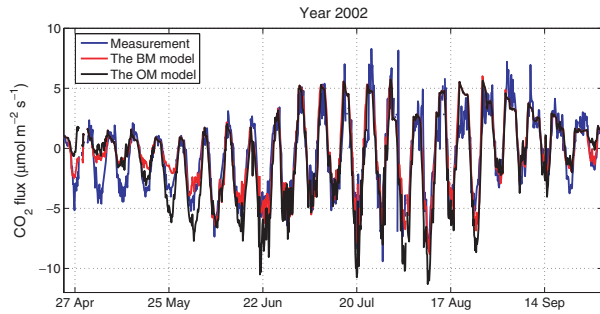


Fig. 6. The weekly averages for diurnal periods for the measurements and the models from the end of April till the end of September in 2002.

During June the BM model was slightly left behind in photosynthesis. This was the time period of the second $V_{c(max)}$ fit. A higher-level fit would possibly produce better results, but the parametrization is necessarily an averaged product due to the variation of the fluxes. For example, June 14 and June 17 were similar bright days having day temperatures around 15°C . The measured flux reached $-7 \mu\text{mol m}^{-2} \text{s}^{-1}$ on June 14 and $-11 \mu\text{mol m}^{-2} \text{s}^{-1}$ on June 17. This difference probably has to do with different source areas, even though the wind direction was approximately northeast during both of these days.

For the rest of the year the CO_2 flux modelled by the BM model succeeded well. Some discrepancy with the measured CO_2 flux was noticed in the first 2 weeks of August. This was caused by a few days with low light levels (below $600 \mu\text{mol m}^{-2} \text{s}^{-1}$) and temperature below 15°C . The forest was photosynthesizing up to $-4 \mu\text{mol m}^{-2} \text{s}^{-1}$, but since at this time a respiration fit with high fluxes was used, the simulation gave upward CO_2 fluxes during daytime. The largest respiration fluxes in July and August were not simulated by the models even when using a fitting time period of 2 weeks.

The OM model performed reasonably throughout the growing season. At the end of May night frosts occurred, and this caused a drop in the daytime CO_2 assimilation fluxes; since β was overestimated at this time, as seen in Fig. 3, the model overestimated the fluxes for about 2 weeks. In addition there was 1 week in July and three at the end of August when the CO_2 fluxes were overestimated. These overestimations were the consequence of very bright days with high PAR fluxes. The OM model did not saturate in high light conditions, and as a result it simulated some very high CO_2 assimilation fluxes. During the last 2 weeks of September the OM model did not attain the measured CO_2 fluxes during cloudy days.

The simulated and measured fluxes for the year 2002 are shown in Fig. 6. During the first weeks shown the BM model was incapable of producing the measured CO_2 fluxes. Spring 2002 was warmer compared to the previous spring and the occurrence of night frosts in May was much rarer. For this reason, during May 2002 the forest had recovered better from its winter dormancy, and was assimilating more at lower temperatures.

As a consequence, the fits for the parameters made for May 2001 were insufficient to provide a good modelled CO_2 assimilation. During the summer period, the BM model performed well.

The OM model performed moderately in 2002. Because of the warmer spring a large part of May remained underestimated. When the last night frost occurred on May 27, the photosynthesis of the forest was highly reduced, and the model overestimated the assimilation. During the last two weeks of September the OM model gave too low assimilation rates on cloudy days.

3.4. Model performance in varying temperature, humidity and light conditions

Residuals can be a helpful tool in assessing the quality of the results. Shown as a function of VPD, they provide information on the effects of stomatal conductance. The residuals were calculated as the modelling results subtracted from the measurement. The residuals of the half-hourly values as a function of vapour pressure deficit are displayed in Fig. 7 for the years 2001 (a, b) and 2002 (c, d) separately for both of the models. Only the daytime values are presented here, the night time values having been excluded by the condition that the measured light level must be above $100 \mu\text{mol m}^{-2} \text{s}^{-1}$. The behaviour of the models as a function of vapour pressure deficit is quite good. Seasonal variance has been observed in the relationship between the conductance and VPD (Medlyn et al., 2002a; Mäkelä et al., 2004; Simon et al., 2005), but Fig. 7 shows that this is not probable for Sodankylä. Overall, water was plentiful for most of the time during the years studied, and the site did not suffer of drought.

The light relationships of the CO_2 fluxes in different temperature ranges show that the OM model simulates too high CO_2 uptake at high light levels (Fig. 8). This overestimation is highest in lower temperatures due to the simulation difficulties in spring. On temperatures less than 10°C the fluxes calculated by BM model are less scattered compared to the measurements. On the temperature range $10\text{--}14.9^{\circ}\text{C}$, there is a group of points underestimated by the BM model on light levels higher than $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$. These points are from early spring. Overall, the BM model appeared to capture the observed light response reasonably. The OM model performed better in this respect on higher temperatures.

A specific time period has been chosen to show the performance of the models on a daily basis. In Fig. 9 six consecutive days in June 2001 are shown with the measured CO_2 fluxes and the modelling results as a function of time, together with the measured relative humidity, VPD, PAR and temperature. In the beginning of June 2001, the measured CO_2 flux was at the typical summer level, reaching $-10 \mu\text{mol m}^{-2} \text{s}^{-1}$. After June 19, daytime values of relative humidity decreased significantly, and the CO_2 flux maximum level fell to a much smaller value, despite there being warm and sunny days, with temperatures reaching about 20°C , conditions usually ideal for assimilation

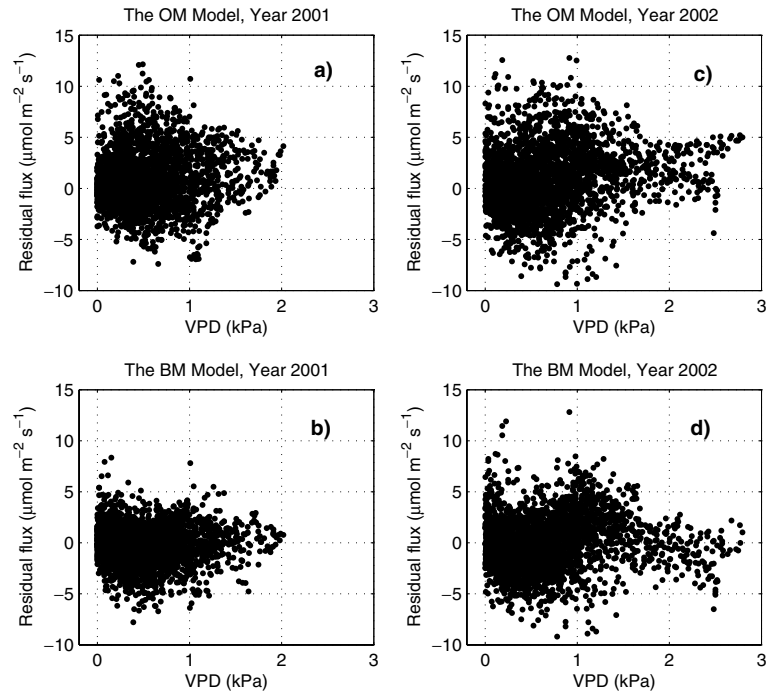


Fig. 7. The residuals for the half-hourly values in the years 2001 (a, b) and 2002 (c, d) as a function of vapour pressure deficit.

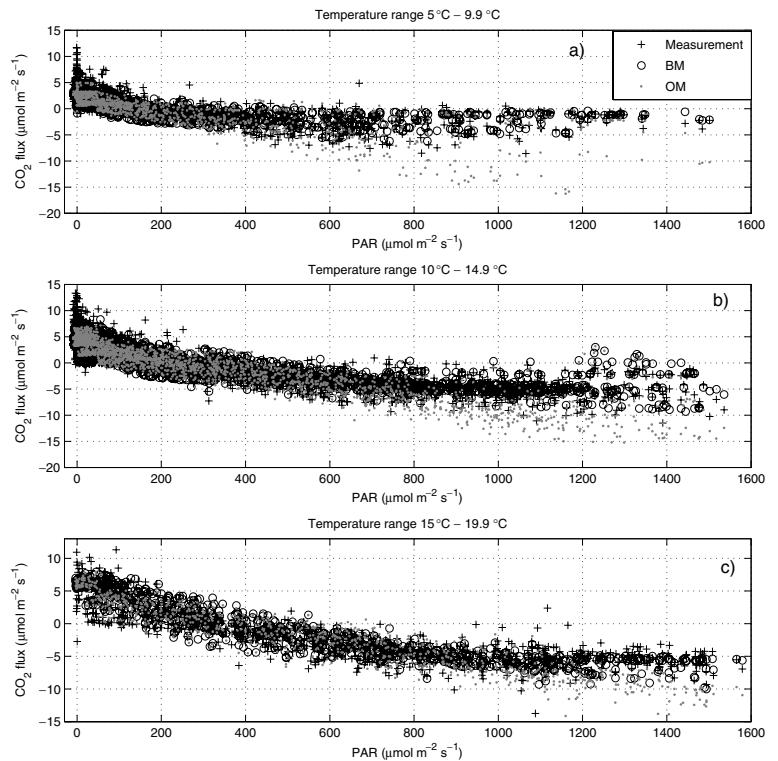


Fig. 8. Light relationships of CO₂ fluxes of the measurement and the two models in three different temperature range: (a) 5–9.9 °C, (b) 10–14.9 °C and (c) 15–19.9 °C.

at Sodankylä. By June 23–24 the exceptionally dry and warm period had already lasted for 5 d, and the measured fluxes started to decrease during the afternoon. During this period, the soil moisture was also quite low. The following night was colder, and during June 25 the relative humidity was higher resulting

in less pronounced afternoon drop in the observed flux. June 27 was a colder day with higher relative humidity, and the measured CO₂ assimilation increased. It also rained on the evening of that day. Assimilation levels returned to the previous higher levels on June 28.

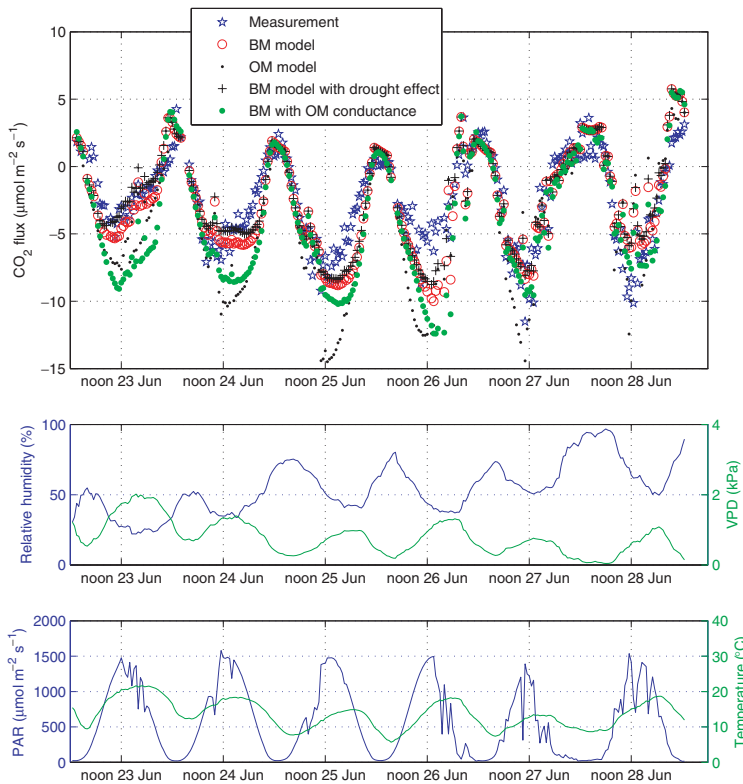


Fig. 9. The measured CO_2 flux and the modelled fluxes by the two models together with the measured relative humidity, VPD, PAR and temperature for 6 d in June 2001. Also CO_2 fluxes calculated with BM model by taking into account drought and by using the OM model conductance are shown.

The models were unable to fully track the June 23–24 afternoon measurements. The BM model simulated a decline in the CO_2 assimilation on June 23 when the relative humidity dropped to below 24%. The OM model also predicted occasional small fluxes during the same afternoon, but these were associated with changes in the light level. On June 24 both of the models missed the drought effect.

On June 25 the BM model produced a higher level of assimilation, due to the change in the $V_{c(\max)}$ parametrization at this time. During June 23–25 the OM model was not clearly affected by the low humidity during the afternoons, and the assimilation rates increased significantly from day to day. The parameter β increased a little with time, but its effect was negligible. The irradiance conditions remained quite constant during this period, while temperatures decreased. The VPD had a significant effect on the maximum photosynthesis rate as simulated by the OM model on days having the same light level, as can be seen in Fig. 8. However, the difference is only seen in daily time steps and the effect of low humidity during afternoons on the CO_2 flux is not simulated.

Also the drought effect was implemented to the model. These model version results are shown also in Fig. 9. On June 23 the high VPD lowered the BM model assimilation to the measured level and this also occurred in the afternoon of June 24. On June 26 the model nevertheless overestimated the CO_2 flux.

The BM model was also run by replacing the Ball-Berry conductance (eq. 5) by the OM model conductance (eq. 8) remaining

the other BM parametrizations unchanged. During the June period, this version of the model exaggerated CO_2 assimilation up to 50% (Fig. 9). In summer the overestimation was usually around 25% when the light level exceeded $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$.

4. Discussion

4.1. Parameter evaluation in the BM model

The seasonality of the BM model parameters has been verified in previous measurements (Williams and Flanagan, 1998; Law et al., 2000; Medlyn et al., 2002a; Kosugi et al., 2003) and its importance in modelling has also been noted in a deciduous forest (Wilson et al., 2001) and a rain forest (Simon et al., 2005). Ogée et al. (2003) also pointed out seasonality's role in the modelling of an evergreen coniferous forest. However, the seasonality is often treated as a trait of $V_{c(\max)}$, with $J_{\max}$ being approximated by a given ratio to it, even though the ratio has been shown to be influenced by seasonality (Medlyn et al., 2002a) and temperature (Leuning, 1997; Walcroft et al., 1997; Leuning, 2002). Usually the ratio of the two parameters is approximately 1.7 (Medlyn et al., 2002b).

For the parameter $J_{\max}$, two different fittings in different seasons were applied and for the parameter $V_{c(\max)}$ three fittings. For $J_{\max}$ the value at 17°C during spring was $40.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ and during summer $61.7 \mu\text{mol m}^{-2} \text{s}^{-1}$. At the same temperature the parameter $V_{c(\max)}$ was in spring $6.0 \mu\text{mol m}^{-2} \text{s}^{-1}$, during

early summer 9.0 and 15.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during late summer. At 17 °C the ratio of $J_{\text{max}}/V_{\text{c(max)}}$ was 6.7, 6.9 and 3.9 in spring, early summer and late summer, respectively. For comparison of these parameter estimates with the literature they were multiplied by π , in order to change from total leaf area to the projected leaf area (Stenberg et al., 1995). For the summer period, the parameters J_{max} and $V_{\text{c(max)}}$ therefore get values at 17 °C of 193.8 and 49.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively.

It was plausible to do these fittings only below 20 °C and therefore we quote the parameter values at 17 °C. The highest temperatures at Sodankylä were less than 28 °C in 2001, and the J_{max} points so few above 20 °C that the transition past the possible temperature optimum of the parameters (Medlyn et al., 2002a) could not be observed.

From the leaf chamber measurements the values we obtained for J_{max} and $V_{\text{c(max)}}$ were 157 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (minimum 144 $\mu\text{mol m}^{-2} \text{s}^{-1}$, maximum 170 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and 75.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (minimum 67.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$, maximum 83.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Their ratio is 2.1, thus agreeing quite well with the literature. These measurements were performed in rather warm conditions (about 27 °C in the leaf chamber) compared to typical growing season temperatures at Sodankylä.

Some estimates of Scots pine parameter values have been made at a temperature of 17 °C at Åheden (Hällgren et al. 1990) by Wullschlegel (1993), that is, 121 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for J_{max} and 46 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for $V_{\text{c(max)}}$; at Värriö, Aalto (1998) estimated values of 95.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for J_{max} and 44.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for $V_{\text{c(max)}}$. According to the Ecocraft project, the parameters at a temperature of 25 °C in Mekrijärvi and Antwerpen were 118 and 314.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for J_{max} , and 60.3 and 121.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for $V_{\text{c(max)}}$, respectively (Medlyn et al., 1999). There is considerable difference between the three northern sites (Åheden, latitude 64°14'N; Värriö, latitude 67°46'N; Mekrijärvi 62°41'N) that are located in the boreal zone to the Antwerpen (latitude 51°10'N) site that is located in the temperate zone. These parametrizations were obtained from leaf chamber measurements.

When the model was run by parameter estimates from Mekrijärvi or our own leaf chamber measurements a large underestimation of assimilation occurred from mid-summer to late summer and this was due to the small value of J_{max} . It has very important role, since it limits the lower portions of the canopy CO₂ flux even in sunny conditions.

The result for the parameter $V_{\text{c(max)}}$ from the canopy level inversion is quite reasonable, while for J_{max} it is quite high, and this is seen in the ratio of these parameters. Despite this, our model worked as expected by switching the most limiting process for photosynthesis according to the environmental conditions, and the estimated J_{max} was not far from the value obtained from the leaf chamber. Because $V_{\text{c(max)}}$ was estimated while J_{max} was kept fixed it might have an effect on differences of their apparent seasonality. Rayment et al. (2002) also iterated J_{max} and $V_{\text{c(max)}}$ for a coniferous forest and obtained results similar to ours. They obtained the parameters at the shoot, branch and canopy levels,

and observed that the canopy level values were the smallest, thus implying optimization of the parameters according to scale.

Our inversion technique yielded the temperature responses of the parameters independently of each other. Often the parameter $V_{\text{c(max)}}$ and the light use efficiency q are determined and the relationship for the parameter J_{max} to $V_{\text{c(max)}}$ is assumed (e.g. Wang et al., 2003). Our results do not support such an approach for Sodankylä. However, there might be some seasonal or temperature-dependent variation in the light use efficiency that is not included in our current model. It might have some influence on the J_{max} values.

The light use efficiency q was taken from shoot chamber measurements at Värriö, another northern Scots pine site. It is not evident that the value is same in Sodankylä and therefore it was investigated in detail. Using q value of 0.07 instead of 0.14 resulted in larger scattering of the inversed BM parameter values and some higher J_{max} values in June. The temperature responses had more scattering and it was not straightforward to do new fittings. However, the old fittings seemed functional. The r^2 value for the year 2001 by q halved was 0.59 and the model underestimated the CO₂ assimilation on a bright summer day by 18%. When the light use efficiency was doubled it did not have a large influence on the temperature responses of the parameters and old fits were used. The r^2 for 2001 was 0.67 with some overestimation of the CO₂ flux occurring. During a bright summer day the CO₂ flux was overestimated up to 16% compared to the earlier modelling result with original light use efficiency.

The BM model parameters have been shown to be correlated to the nitrogen content of plants (Field, 1983; Harley et al., 1992; Walcroft et al., 1997), thus making the model parameters vary according to season, needle age and the vertical gradient of nitrogen content in the sunlit and shaded leaves of the canopy (Kellomäki and Wang, 2000; Meir et al., 2002; Eichelmann et al., 2005). Often the variation of BM model parameters and simultaneously the nitrogen content are approximated by the light gradient (Sellers et al., 1992) in the vertical direction, as was also done in our modelling, but evidence against this method has also been presented (Evans, 1989; Rayment et al., 2002). According to Hollinger (1996), the approach of Sellers et al. (1992) overestimates the canopy assimilation by 5–10%.

Compared to the literature values (Wang et al., 1996) our J_{max} during the latter part of the summer was large at temperatures higher than 10 °C. When we run the model by using the literature values there was a total failure of the model to simulate the CO₂ fluxes with over 65% underestimation on bright days during July and August. On the other hand, June was simulated reasonably and our $V_{\text{c(max)}}$ estimation was close to the literature's temperature response curve. When we adapted temperature response estimated from Hyytiälä leaf chamber measurements (Aalto, 1998), very similar results were obtained, with the exception that because the J_{max} was even lower the late summer time CO₂ fluxes were more strongly underestimated. The difference between literature values and our inversion results

brings out the need for these larger scales estimations of the parameters.

4.2. Parameter evaluation in the OM model

The OM model did not saturate at high light levels, which might be caused by the parameter γ (eq. 7). γ was estimated from shoot gas exchange measurements on shoots at Värriö, northern Finland (Kolari et al., 2007). This discrepancy of the model might be due to the change in scale or in the parametrization procedure for γ . This shows a clear difference between the models, since the $V_{c(max)}$ values in the BM model ensure that the model saturates at high light levels. The effect of drought is also not simulated well by the OM model, which might be partly induced by the simple parametrization of λ (eq. 8) and the dependence of the drought effect on VPD in the conductance of the model.

The other ways to parametrize β (leaf chamber measurements and the so-called state of acclimation) did not provide a clearly better way for the parametrization than the seasonal polynomial fit. The chamber measurements were not conducted at Sodankylä, and it was not obvious that they can be used directly in this context. The β estimated from eddy measurements performed better than that estimated from the leaf chamber data, while the state of acclimation performed equally as well as our estimated β . Estimation of β from eddy covariance measurements is thus not necessary, since an estimate based solely on temperature is equally good.

During the summer time the OM model is mostly driven by the amount of light. The temperature response of photosynthesis enters the model more or less indirectly via the parameter β during the periods of transition to summertime. On the other hand, in the BM model the two main parameters have a very strong temperature response. The light level influences switching between the two most limiting processes for photosynthesis in the model and the RuBP regeneration-limited rate of photosynthesis has a light dependency. However, Sodankylä is a site with very strong temperature variations and this should thus be a significant factor in the modelling efforts. For such a northern site, a good parametrization at lower temperatures is essential, since those fluxes have a major influence on the annual GPP value.

4.3. Respiration and conductance experiments

In Sodankylä the total ecosystem respiration increased to a higher level after mid-summer during both years. The reasons for level changes in respiration are not self-evident. The changes in the microbial population of the soil could have some effect (Sacks et al., 2006) or the phenomenon could be caused by the dynamics of the roots or fine root growth. The nature of respiration could be studied more closely by a full soil model. The simple parametrizations used here could maybe be scaled to levels high enough, but it would not be reasonable for the functioning of the current ecosystem model as a whole. Nevertheless, soil and stem

respirations, which must be subtracted from the micrometeorological net fluxes, are a major source of uncertainty when model parameters are deduced from ecosystem scale observations.

The June drought period brought further out the need for a soil model. On June 23 the stomatal conductance was lowered during afternoon [see e.g. Kellomäki and Wang (2000) for similar observations at a Finnish Scots pine forest at Mekrijärvi] and the stomatal conductance was limiting the carbon assimilation (see e.g. Brooks et al., 1997). However, at such low relative humidities the Ball-Berry conductance model often produced unrealistic results. On June 24 the BM model missed the drought effect, suggesting a need for careful parametrization of the Ball-Berry conductance at very low humidity levels and for the addition of a soil model to the canopy scale model to account for a possible drought effect in the conductance. A coefficient which lowered the Ball-Berry conductance as a function of increasing VPD improved the results slightly, but it would be better to take into account the length of the drought period and therefore the soil conditions. The OM model was not able to react to the drought. When the conductance part of the OM model was combined to the photosynthesis part of the BM model the same phenomenon was seen. It would be important to parametrize the OM model more carefully, both γ and λ .

4.4. Conclusions

We successfully parametrized the BM model by using the ecosystem scale eddy covariance data. The parameters obtained by this method may include some other effects but their stability and clear temperature responses indicate that this is a feasible way to obtain them. They did not correspond well to the leaf-level measurements, but those leaf-level measurements were scarce and did not describe the whole forest. Discrepancy between derived and measured parameters is worth further studies. For the OM model, parametrization from eddy covariance data is not necessary because reasonable results are obtained by using the temperature-tied state of acclimation.

Empirical models often yield better results than the mechanistic models. Our results show that seasonal optimization and derivation from eddy covariance of the parameters of the mechanistic model can outperform the pure empirical model. Our achievement was that we obtained large-scale parametrization for the BM model as well as the different temperature responses for the parameters varying according to the season. These provide possibilities to investigate the biological state of the forest deeper, especially when done simultaneously with other flux sites. Seasonally varying temperature response functions for the model parameters would be very laborious to obtain by leaf chamber measurements.

At Sodankylä, the ratio of the two BM model parameters was not the same as that found in the literature. The possible effect of the light quantum yield in the value of J_{max} should therefore be studied more carefully. The radiative transfer model used and

its parametrizations might also have a significant impact on the photosynthesis parameters; this should be studied by comparing different radiative transfer models with a variety of parametrizations.

For the parametrization of the BM model, the method could be improved by finding a way to combine different fittings for different states of the photochemical efficiency of the canopy during the transition periods towards the summer. This could be linked with some kind of temperature index employing night frosts or with the chlorophyll fluorescence F_v/F_m . Because this is lacking in the current modelling, the BM model failed in May 2002. The slowing down and drawback of spring recovery due to the frequency and severity of the night frosts has been modelled by Bergh et al. (1998) and their approach might also be useful in our modelling. The capability of F_v/F_m in modelling seasonality has been discussed by Nippert et al. (2004). Measurements of F_v/F_m have been performed at Sodankylä for several years.

The values of the two BM model parameters are commonly quoted for a temperature of 25 °C. However, at Sodankylä such a high temperature occurs only rarely during the growing season so it was not possible to parametrize the BM model for high temperature range. It is not obvious how the temperature responses for the parameters function on high temperatures. In leaf chamber measurements conducted in Finland in three Scots pine forest the temperature optimum for $J_{\max}$ has been lower than 20 °C (Wang et al., 1996; Aalto, 1998) and also $V_{c(\max)}$ has been shown to have a temperature optimum in Finland (Wang et al., 1996).

The eddy covariance results are quite scattered. By its nature, eddy covariance is a large-scale measurement and includes effects caused by turbulence. In the eddy covariance technique, the measurement error is approximately 10–20% (e.g. Moncrieff et al. 1996, Aubinet et al. 2000). The model inversion included up-scaling, but understandably this cannot be done perfectly. Possible error sources are to be found in inaccuracy in the radiative transfer modelling, in estimation of the vertical distribution of the carboxylation efficiency, heterogeneity in the stand structure, night-time respiration fluxes, absence of stem respiration, soil water effects, etc.

The most important improvement to the model would be to better separate the assimilation and respiration fluxes; using data from an eddy covariance system below canopy level would be a good tool for this. This would also help to remove the effect of the underground vegetation. Below-canopy EC measurements have already been conducted at the Sodankylä site.

5. Acknowledgment

We gratefully acknowledge the friendly co-operation of the personnel at the Arctic Research Centre of the Finnish Meteorological Institute at Sodankylä, as well as the financial support from the Academy of Finland and the Nordic Council of Ministers.

Table 4. The parameters of the radiative transfer model (Sellers, 1985), taken from Knorr (1997)

Definition	Symbol	Value
Leaf single scattering albedo	Ω	0.12
Forward scatter factor for the diffuse flux	β	0.5
Forward scatter factor for the direct flux	β_0	0.5
Extinction coefficient for the direct flux	K	0.5
Mean of K^{-1} over the downward hemisphere	M	1

Also we thank Dr. Ismael Moya for borrowing LI-COR 6400 and Mr. Jarno Kallonen for the forest inventory. The authors also gratefully acknowledge two anonymous reviewers for their constructive comments.

6. Appendix A

A.1. Up-scaling of the models to the canopy scale

The parameters used in the two-stream flux radiative model as adopted from Knorr (1997) are displayed in Table 4. Here an isotropic leaf distribution and equality of leaf reflectivity and transmissivity were assumed. The daily albedo was calculated by taking the ratio of the half-hourly values of upwards- and downwards-directed PAR measurements, and taking the median of these values during the 6 h around midday.

The BM model parameters were assumed to diminish proportionally to the percentual photosynthetically active radiation (Sellers et al., 1992; Kull and Jarvis, 1995), and were calculated as

$$p = p_0 f \text{ PAR} / k_L, \quad (\text{A1})$$

where p is the parameter value at a certain height, p_0 is the magnitude of the parameter at a given temperature, and $f\text{PAR}$ is

$$f\text{PAR} = (1 - e^{-k_L L_t}), \quad (\text{A2})$$

where L_t is the total leaf area index of the canopy and k_L is the extinction coefficient for light with cumulative LAI defined as

$$k_L = k_D D / L_t, \quad (\text{A3})$$

where D is the depth within the canopy and k_D is the extinction coefficient with canopy depth, assumed to be 0.5.

The sunlit and shaded portions of the canopy in different layers were estimated by a method proposed by Thornley (2002). The sunlit part of the foliage L_{sun} in different layers, denoted here by subscript i , is calculated as

$$L_{\text{sun},i} = \frac{1}{k} (1 - e^{-k L_i}), \quad (\text{A4})$$

where k is the extinction coefficient and L_i is the cumulative leaf area index at that height, increasing as one descends into

the canopy. $L_{\text{sun},i}$ is then multiplied by the leaf area index of the layer. The shaded part of the foliage at a specific height is the remainder.

The sunlit and shaded parts were computed separately when calculating the conductance and the A_j -limited CO_2 assimilation branch in the BM model. In the sunlit part the foliage received the direct and diffuse radiation fluxes, whereas the shaded part received only diffuse radiation, as calculated by the radiative transfer model.

7. Appendix B

B.1. The respiration values

The respiration was divided into foliar and soil respiration. The foliar respiration at 10 °C was estimated from leaf chamber measurements. The temperature response was adapted from Lloyd and Taylor (1994) and was

$$R = R_{10} e^{E_0 \left(\frac{1}{283.15 - T_0} - \frac{1}{T - T_0} \right)}, \quad (\text{B3})$$

where T is temperature, R is the respiration rate and E_0 and T_0 are parameters that were also taken from Lloyd and Taylor (1994). The fitted parameters for foliar respiration are displayed in Table 5.

The same Arrhenius-type dependency was used for the estimation of the soil respiration as for the foliar respiration. The soil respiration was estimated from the night-time CO_2 eddy covariance flux measurements by fitting a function to the air temperature response of the flux for sequential time-periods of two weeks during the growing season. At the same time the foliar respiration was reduced from the measured respiration flux. The air temperature was used in this case instead of the soil temperature, because it has been proven in some cases to give the most reliable temperature–respiration relationship (van Dijk and Dolman, 2004) and suited best with our measurement results.

The foliar respiration was present in the formulations of the photosynthetic gas exchange models. When scaling up to the canopy level the soil respiration was always subtracted from the modelled assimilation rates.

Table 5. The parameters used in the foliar respiration (eq. B3)

	Symbol and unit	Value
Foliar respiration	R_{10} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1.3636
	E_0 (K)	308.56 ^a
	T_0 (K)	227.13 ^a

^aLloyd and Taylor (1994).

8. Appendix C

C.1. Studying the performance of the models

To quantify the performance of the models, the goodness of fit and root mean square errors were computed. The correlation coefficient r was defined as

$$r = \frac{\sum (y_p - \bar{y}_p)(y_o - \bar{y}_o)}{\sqrt{\sum (y_p - \bar{y}_p)^2 \sum (y_o - \bar{y}_o)^2}}, \quad (\text{C1})$$

where y_p is the predicted value and y_o the observed value. The correlation coefficient squared, r^2 , gives us the goodness of fit.

The definition used for the RMSE was

$$\text{RMSE} = \sqrt{\frac{\sum (y_o - y_p)^2}{N}}, \quad (\text{C2})$$

where N is the number of observations.

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