

Assessing seasonality of biochemical CO₂ exchange model parameters from micrometeorological flux observations at boreal coniferous forest

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Abstract. The seasonality of the NEE of the northern boreal coniferous forests was investigated by means of inversion modelling using eddy covariance data. Eddy covariance data was used to optimize the biochemical model parameters. Our study sites consisted of three Scots pine (*Pinus sylvestris*) forests and one Norway spruce (*Picea abies*) forest that were located in Finland and Sweden. We obtained temperature and seasonal dependence for the biochemical model parameters: the maximum rate of carboxylation ($V_{c(\max)}$) and the maximum rate of electron transport (J_{\max}). Both of the parameters were optimized without assumptions about their mutual magnitude. The values obtained for the biochemical model parameters were similar at all the sites during summer time. To describe seasonality, different temperature fits were made for the spring, summer and autumn periods. During summer, average J_{\max} across the sites was $54.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ (variance $31.2 \mu\text{mol m}^{-2} \text{s}^{-1}$) and $V_{c(\max)}$ was $12.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ (variance $6.6 \mu\text{mol m}^{-2} \text{s}^{-1}$) at 17°C . The sensitivity of the model to LAI and atmospheric soil water stress was also studied. The impact of seasonality on annual GPP was 17% when only summertime parameterization was used throughout the year compared to seasonally changing parameterizations.

1 Introduction

According to scenarios of future climate, the boreal forest zone is expected to experience a larger increase in temperature than other regions (Trenberth et al., 2007). Comparison across the latitudinal spread of boreal forest is therefore important, so that it is possible to predict how the northern forests will behave in the future, and what effects the future climate might have on their carbon balance. In our study we have investigated the boreal sites at different latitudes and how modelling of their gas exchange can be improved.

In order to obtain estimates for large-scale carbon sinks, it is important that the global and regional models are parameterized using a sufficiently good method. Large-scale models often use photosynthesis parameters that have been estimated at the leaf level and then scaled to the canopy level (Sellers et al., 1996). Wang et al. (2006) pointed out that this is not the most reliable way since the up-scaling procedure introduces errors. Therefore it is essential to parameterise photosynthesis models also on the larger scale, taking advantage of the widespread eddy covariance flux tower network.

A biochemical model based on a mechanical description of photosynthesis was developed by Farquhar et al. (1980) and will henceforth be referred to as the biochemical model. The biochemical model is widely used in modelling on various scales (Juurola et al., 2005; Knorr and Kattge, 2005). It has several important parameters and in this study we will focus on two of them: the maximum carboxylation rate ($V_{c(\max)}$) and the maximum potential electron transport rate (J_{\max}). Global models do not usually take into account the seasonality of the temperature-dependent photosynthesis parameters. These have been shown to be affected by seasonality (Dang



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Table 1. Characteristics of the measurement sites

Site	Location	LAI (m ² /m ²) (all-sided, annual)	Mean annual temperature (°C) and precipitation (mm) (30 year average)	Canopy height (m)	Measurement height (m)	References
Kenttäröva	67°59' N 24°15' E	6.6	−1.7 450	13	23	Aurela (2005) Finnish Meteorological Institute (1991) Aurela (2005)
Sodankylä	67°21' N 26°38' E	3.6	−1.0 500	12	12	Aurela (2005)
Hyytiälä	61°51' N 24°17' E	8.0	3.0 709	13	13.3	Markkanen et al. (2001) Vesala et al. (1998, 2005)
Norunda	60°5' N 17°28' E	13.5	5.5 527	28	35	Grelle et al. (1999)

et al., 1998; Xu and Baldocchi, 2003; Han et al., 2004), even though this has not always been noticed in boreal forests (Wang et al., 2006).

In cold climate regions, the photosynthesis in forests does not immediately reach its full capacity at the beginning of the active season. It may take several weeks before the damage caused by low winter temperature is fully repaired (e.g., Pelkonen and Hari, 1980). Thus, the transition period from winter dormancy to full photosynthetic capacity plays a significant role in altering the carbon balance of northern boreal coniferous stands (Bergh et al., 1998). A field study by Bergh and Linder (1999) of Norway spruce concluded that the spring recovery was mainly controlled by mean air temperature and severe night frosts. The importance of mean air temperature for spring recovery was also shown by Tanja et al. (2003). In their study they used eddy covariance data from boreal sites; their objective was to find the average air temperature that raises the photosynthesis to a level of 20% of the maximum summertime fluxes.

Our aim was to study the seasonality and transition periods of northern forests by means of biochemical model parameters estimated from micrometeorological observations. Model parameters were deduced from CO₂ flux observations by inverting a canopy photosynthesis model. Our motivation was to study whether the phenomenology of larger-scale models can be improved.

We parameterized a canopy-scale model that was upscaled from the leaf level in order to obtain the parameters $V_{c(\max)}$ and J_{\max} for four different coniferous forest sites, all located in the boreal zone. The parameterization results for the different sites were intercompared. The relations between air temperature and the biochemical model parameters over the whole growing season were assessed. Also, it was investigated whether temperature indices could be used in improving the seasonality of the biochemical parameters in the modelling. The sensitivity of the model to various aspects was also studied.

2 Materials and methods

2.1 Measurement sites and measurements

We studied four conifer forests that were located in the boreal zone. Two sites, Kenttäröva and Sodankylä, are situated in northern Finland and in the northern boreal zone (Solantie, 2005). The Sodankylä site is a Scots pine (*Pinus Sylvestris*) forest. Kenttäröva is a homogenous Norway spruce (*Picea abies*) forest. The Scots pine-dominated forest at Hyytiälä is in the southern boreal zone in Finland. The southernmost site of Norunda is in the hemi-boreal zone in the central part of Sweden. Norunda is a mixed Scots pine/Norway spruce coniferous forest. More detailed descriptions of the sites are to be found in Table 1 and in Lindroth et al. (2008). Leaf area index (LAI) in Table 1 is the total (all-sided) LAI.

We used at least two years of data from each of these sites: Hyytiälä 2000–2001, Sodankylä 2001–2005 and Norunda 1999, 2001 and 2002. For these three sites the year 2001 was used for the model parameterization. To study the spruce forest of Kenttäröva, we used data for the years 2003–2006, the latter year 2006 being used for parameterization.

Net fluxes of momentum, sensible and latent heat and carbon dioxide fluxes were measured by the eddy covariance method using fast-response sonic anemometers and closed-path IRGAs. Measurement heights were at least three metres above the highest trees. Other meteorological variables measured included Photosynthetic Photon Flux Densities (PPFD), air temperature, relative humidity, air pressure and precipitation.

2.2 Modelling and data analysis

A canopy-level gas exchange model was parameterized by inversion from the canopy CO₂ flux data. The leaf level CO₂ gas exchange model was based on a formulation first introduced by Farquhar et al. (1980) and Farquhar and von Caemmerer (1982) with later modifications (De Pury and Farquhar, 1997). The biochemical model has a RuBP

regeneration-limited rate (A_j) and a Rubisco activity-limited rate (A_c), of which the minimum of the two governs the photosynthesis A :

$$A = \min \{A_j, A_c\}. \quad (1)$$

A_j -assimilation is

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

and A_c -assimilation is described as

$$A_c = V_{c(\max)} \frac{c_i - \Gamma^*}{k_c(1 + o/k_o) + c_i} - R_d \quad (3)$$

In these two equations $V_{c(\max)}$ is the maximum rate of carboxylation, 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. J is the potential electron transport rate:

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

It is a function of incident irradiance (I_o), the light use efficiency factor (q), the convexity of the light response curve (Θ) and J_{\max} , the maximum rate of electron transport.

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). For some species $V_{c(\max)}$ and J_{\max} have an Arrhenius-type temperature dependency (Harley and Baldocchi, 1995):

$$f_T = f_0 \exp \left[\frac{E_f(T - 290.15)}{290.15RT} \right] \quad (5)$$

where f_0 , the base rate, denotes the parameter ($V_{c(\max),\text{std}}$ or $J_{\max,\text{std}}$) at 17°C, E_f is the activation energy, R is the gas constant and T is temperature in Kelvin.

The Ball-Berry conductance model (Ball et al., 1987) was used in conjunction with the biochemical model for describing the stomatal conductance. The conductance g_{BB} is described as

$$g_{BB} = g_o + g_1 \frac{RH * A}{c_a} \quad (6)$$

where RH is the relative humidity, A is the assimilation rate, c_a is the ambient CO₂ concentration and g_o 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 (Thum et al., 2007). Mesophyll conductance is also shown to be important (Juurola et al.,

2005) but it was difficult to estimate the mesophyll conductance for the whole forest and therefore we assumed infinite mesophyll conductance.

The model and its up-scaling are described in detail in Thum et al. (2007). In order to up-scale the leaf-level model to the canopy scale, a vertical profile of the leaf area distribution was constructed individually for each site with the help of the beta distribution (Wu et al., 2003). The forest canopy was divided into four layers, with equal biomass in each layer. The radiative transfer by Sellers (1985) was used for radiation calculations. The biochemical model parameters were assumed to decrease with height above the ground proportionally to the percentual PPFD, similarly to the nitrogen content (Sellers et al., 1992; Kull and Jarvis, 1995). The leaf layers were also separated into sunlit and shaded parts, according to Thornley (2002). The vertical biomass distribution was different from site to site, but other model parameters, e.g., radiation parameters and light use efficiency q , were kept constant in this study (see Thum et al., 2007).

2.3 Respiration

For calculation of Gross Primary Production (GPP), we subtract soil and needle respiration (R_{soil} and R_{needle}) from the ecosystem assimilation (A_{eco}):

$$GPP = A_{\text{eco}} - R_{\text{soil}} - R_{\text{needle}}. \quad (7)$$

Needle respiration values for the two sites located south of the Arctic Circle were estimated from the Hyytiälä shoot chamber measurements (Kolari et al., 2007). For Sodankylä, too, the needle respiration was estimated from shoot chamber measurements (Thum et al., 2007). For Kenttäröva, the needle respiration was taken from the literature (Stockfors and Linder, 1998), using needle dry weight data measured at the site (Steinbrecher et al., 1999).

First, the needle respiration was subtracted from the night-time flux measurement, after which the soil respiration was fitted to the night-time flux measurement data using the temperature response presented by Lloyd and Taylor (1994). Air temperature was used, since it had a more continuous time series than soil temperature and it gave good results. The fittings were made to biweekly data sets, and both of the two parameters (respiration at 10°C and the activation energy) were fitted. The soil temperature might better represent respiration during snow melt but this effect weakens during two week long fitting periods. At Hyytiälä a response function based on both air and soil temperature introduced by Markkanen et al. (2001) was used, since a continuous time series in soil temperature was available at Hyytiälä and the fit yielded good results.

Table 2. The fitting parameters f_0 and E_f for J_{\max} and $V_{c(\max)}$ from Eq. (5) for all the time periods in the parameterization year at 17°C. The parameter f_0 is the value of the parameter J_{\max} or $V_{c(\max)}$ at 17°C. Also the value of the biochemical model parameter at 20°C and 25°C shown for each fit.

Site	f_0	E_f (J mol ⁻¹)	value at 20°C	value at 25°C
Parameter J_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)				
Sodankylä				
Spring (1 May–3 June)	40.3	83 045	57.4	101.5
Summer (4 June–30 September)	61.7	75 002	84.8	142.1
Kenttäröva				
Spring (May)	31.6	72 779	43.1	71.0
Summer (June–August)	51.3	61 259	66.5	101.4
Norunda				
Spring and summer (April–October)	54.1	88 014	78.6	144.0
Hyytiälä				
Spring (April)	5.6	9151	5.8	6.2
Summer (May–August)	48.8	64 949	64.3	100.5
Autumn (September)	29.5	34 085	34.1	43.1
Parameter $V_{c(\max)}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)				
Sodankylä				
Spring (1 May–3 June)	6.0	75 531	8.3	13.9
June (4 June–24 June)	9.9	79 236	13.0	23.6
Summer (25 June–August)	15.8	84 181	22.6	40.3
Kenttäröva				
Spring (May)	6.1	68 027	8.1	13.0
Summer (June–August)	10.5	64 432	13.8	21.5
Norunda				
Spring (1 March–19 April)	1.9	28 199	2.1	2.6
Summer (20 April–30 September)	11.2	73 616	15.3	25.4
Hyytiälä				
Spring I (April)	1.58	311.5	1.59	1.59
Spring II (May)	3.9	14 841	4.1	4.6
Summer (June–August)	10.4	78 852	14.5	25.0
Autumn (September)	8.7	50 164	10.8	15.2

2.4 Fitting procedure

A parameterization year was chosen, and temperature responses for the biochemical model parameters J_{\max} and $V_{c(\max)}$ were obtained from the inversed CO₂ flux data. All the other parameters (Θ , q , k_c , k_o , Γ^* in the Farquhar model) were kept fixed during the inversion, since the focus of this study was on J_{\max} and $V_{c(\max)}$. For estimating the biochemical parameters, a procedure introduced by Lloyd et al. (1995) was used: The measured CO₂ flux points from late morning were used in the inversion. Measurements with light levels between 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ were used to obtain the temperature response for the parameter J_{\max} . To estimate the parameter $V_{c(\max)}$, measurements at higher light levels and the fit found for the parameter J_{\max} were used. During optimization of $V_{c(\max)}$ the uppermost layer in high light was A_c -limited and the lower canopy lay-

ers were restricted by the minimum of A_c - and A_j -limited assimilation. Inversed parameter values were plotted as a function of temperature, and Arrhenius-type fittings (Eq. 5) were performed.

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. One variable was minimized in estimation of the biochemical model parameters J_{\max} and $V_{c(\max)}$. 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. Two variables were

minimized when the temperature responses were fitted and three variables when J_{\max} , $V_{c(\max)}$ and q were minimized synchronously.

To compare the values of the inversed parameter values to the literature, we needed to multiply our values by π (here π refers to the mathematical constant, its value being approximately 3.1416). This multiplication takes into account the shading caused by the structure of the conifer needle itself and clumping of the foliage (Stenberg et al., 1995).

Since some temporal pattern appeared in the temperature dependencies of the inversed values, several temperature fittings were performed for the year instead of using only one. To select the time periods for different fittings, the general locations of the parameter values on the temperature response were investigated. When the parameter values from the springtime were on a lower level than the summertime values, a separate temperature response was made for the springtime values. The so-called changeover dates are the days when the temperature fit for one period is switched to that for the next, e.g., from spring to the summer period. To determine the changeover date, the time period between spring and summer period was studied. It was experimented whether the temperature response made for the spring or the summertime yielded better results. The first day when the fit for the summertime functioned better was the changeover date from springtime to summertime.

We also improved the modelling of seasonality by using temperature indices. The spring recovery of forests is more dependent on temperature than on the calendar date. Moving the changeover dates according to temperature might improve modelling results during other years compared to keeping the dates the same as those in the parameterization year. To test this, we used the temperature sum, which is the sum of positive daily average temperatures (Solantie, 2004) and the five-day running average temperature (Tanja et al., 2003).

3 Results

3.1 The parameterization at different sites

We obtained plots for temperature dependencies from model inversion. Our results indicated exponential temperature response of the biochemical model parameters at our sites, thus justifying the use of Eq. (5). After analyzing these results and the functioning of the model, using multiple temperature dependencies for the parameters appeared as a feasible step forward. These different responses changed according to the season, and different time periods were used for each of the sites. At all sites, the inversed spring values for parameter $V_{c(\max)}$ were at a lower level than the summertime values, and therefore another fit was made for the spring time. For three sites, different fittings for J_{\max} were also performed separating the spring and summer periods.

The fitting parameters are shown in Table 2 together with the values of the biochemical parameters at 20°C and 25°C. In the summertime fits, the values for $J_{\max, \text{std}}$ (the base rate f_0 of the parameter J_{\max}) vary between 48.8 and 61.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which is not a large variation, considering the latitudinal spread between the different sites. The value of the parameter $V_{c(\max), \text{std}}$ at 17°C (the base rate f_0 of the parameter $V_{c(\max)}$) had a relatively larger fluctuation in summertime: between 10.4 and 15.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

In Fig. 1a and b the temperature responses of J_{\max} and $V_{c(\max)}$ and their fittings are displayed for the northernmost site, Kenttäröva, in the year 2006. For the Kenttäröva site, it was feasible to produce two temperature responses for both of the biochemical parameters. The springtime fitting period was May, when photosynthesis started. The estimates of J_{\max} and $V_{c(\max)}$ found in May were lower than those during summer, and they still had a temperature dependency. Some J_{\max} late summer points were also low, but better modelling results were not obtained by using the spring fit during that time.

The temperature responses of the parameters and their fittings for Sodankylä are shown in Fig. 1c and d. For this site, the year 2001 was used for the seasonal temperature-dependence parameterization. Two fits were made for the parameter J_{\max} . The changeover date was determined by the change in magnitude of the daily values and the simulation results of the model. The change between the spring and summer regimes was estimated to occur on 4 June. In the parameterization of $V_{c(\max)}$, a similar spring fit was made, as well as an additional fit for the transition period from 4 June to 24 June.

Using the chronologically-extensive Hyytiälä database, it was feasible to divide the growing season of 2001 into three periods for J_{\max} and four for $V_{c(\max)}$ according to the season. These are shown in Fig. 1e and f. For the parameter J_{\max} , a separate fit was made for springtime until the end of April, and again for the autumn beginning on 1 September. During spring, the values were hardly temperature dependent at all, whereas the autumn values slowly rose with temperature. The $V_{c(\max)}$ results were not temperature dependent either in April or May, but in the latter month the values were larger. The autumn values increased with temperature, but slower than the summer values. With these fits the model worked best when compared to the measurements.

For Norunda the inversed parameter values were quite scattered (Fig. 1g and h). There were no early spring values for the parameter J_{\max} and therefore it was not possible to perform a fit for this time period separately. A single fit for the whole growing season was therefore used for J_{\max} . During March and the first half of April the observations of $V_{c(\max)}$ were at a lower level, and a separate fit for this time period was done. For the rest of the growing season from 20 April onwards only one fit for $V_{c(\max)}$ was made.

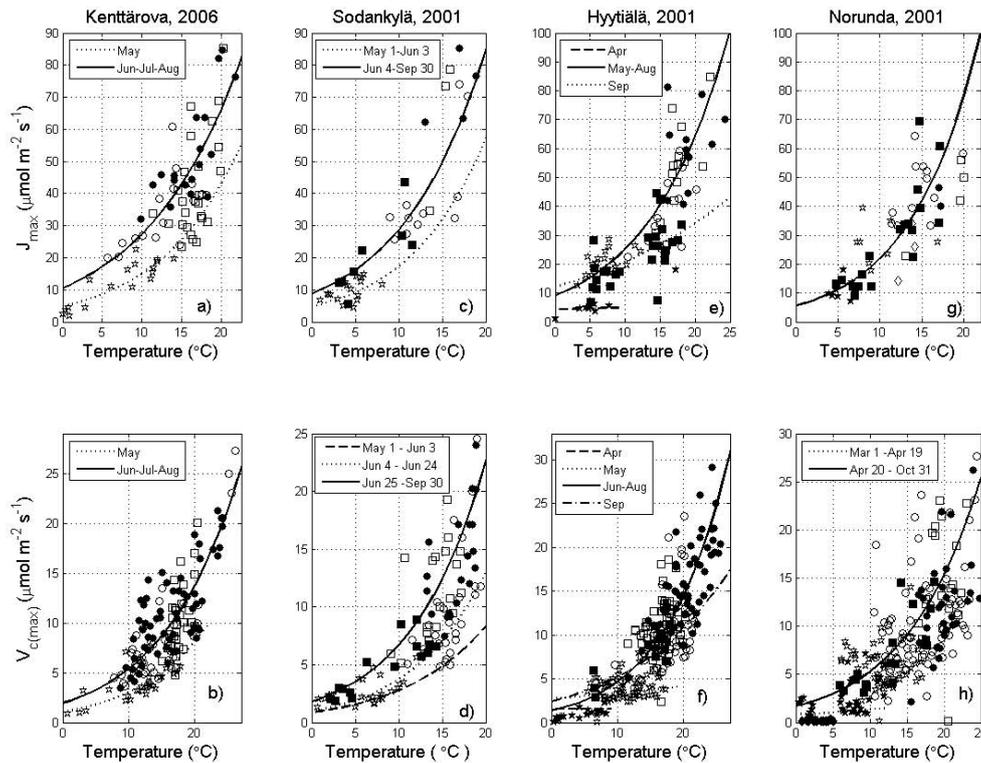


Fig. 1. The temperature responses of the biochemical model parameters J_{\max} and $V_{c(\max)}$ at Kenttäröva in 2006 (a) and (b), at Sodankylä in 2001 (c) and (d), at Hyytiälä in 2001 (e) and (f) and at Norunda in 2001 (g) and (h). The points were obtained by model inversion from half-hourly eddy covariance data. Filled diamonds denote points in March, filled stars in April, empty stars in May, empty circles in June, filled circles in July, empty squares in August, filled squares in September and empty diamonds in October. The time periods of the temperature fits are shown in the legends.

As a result, we got several temperature dependencies for J_{\max} and $V_{c(\max)}$ for different sites. Model performance (NEE) during the whole growing season in the various years was studied resulting in r^2 values between 0.58 to 0.81, Norunda being lowest and Hyytiälä highest (data not shown). The model had similar r^2 in those years that were not used for the parameterization.

3.2 Linking J_{\max} and $V_{c(\max)}$ parameterizations to temperature indices

In Fig. 2 the annual cycle at Kenttäröva in 2006 is shown. ΔJ_{\max} in Fig. 2a is the difference between the mean of the inverted late morning values of J_{\max} and value given by the temperature dependency for the late morning mean temperature. $\Delta V_{c(\max)}$ is the corresponding value for the $V_{c(\max)}$ parameter (Fig. 2a). The five-day floating average temperature (5Dave), the minimum temperature as well as the CO₂ flux from the eddy covariance measurements are also shown (Fig. 2b, c). The springtime temperature response is valid until end of May (Day Of Year (DOY) 152). There is a severe night frost occurring before 20 May (DOY 140) and this

can be seen as a slight decrease in both of the biochemical parameters as respect to the value given by the fitted temperature dependency.

As a result of the optimizations the sites obtained several temperature responses for the biochemical parameters, as was seen in Fig. 1. The time periods for these temperature responses were based on the inversion results during the parameterization year. Since different years are not similar e.g. in respect to the spring recovery, this kind of parameterization caused, for example, an underestimation of the fluxes in Sodankylä in the springtime of 2002, which was warmer than the previous spring. In order to investigate whether temperature indices can be useful here, we linked them with the changeover dates of temperature responses and investigated the resulting simulated CO₂ fluxes.

We used 2002 at Sodankylä and 2000 at Hyytiälä as our test years. The temperature sum and the 5Dave were used to as proxies to describe the photosynthetic state of the vegetation (Tanja et al., 2003). We took the values of these two temperature indices on the changeover dates in the parameterization years and located them in the test years. During spring the use of temperature sum yielded better results compared to

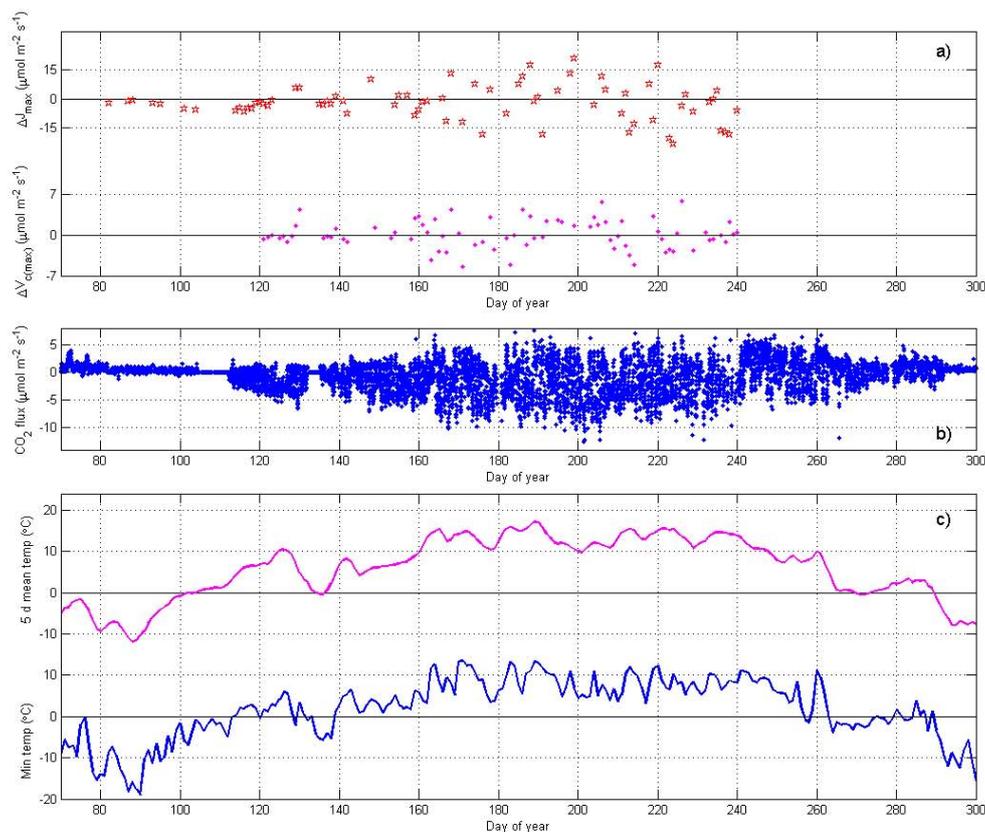


Fig. 2. Various parameters for Kenttäröva in 2006 as a function of day-of-the-year. **(a)** Difference between value from the temperature fit for the parameter and the inverted daily values of the biochemical parameters J_{\max} (red symbols) and $V_{c(\max)}$ (magenta symbols); **(b)** eddy covariance flux measurements; **(c)** five-day average air temperature (magenta line) and minimum air temperature (blue line). Negative CO₂ fluxes denote uptake by vegetation and positive CO₂ fluxes respiration.

the calendar date fixed changeover dates at both sites. Same applied for the new changeover dates estimated by 5Dave, its problem being that the dates were not always uniquely defined. These two methods also gave similar changeover date in the autumn at Hyytiälä in 2000 but due to data gap it was not possible to evaluate if using these new changeover dates would improve simulation results.

3.3 Sensitivity of modelled fluxes to changes in LAI and biochemical parameters

In the sensitivity analysis, the effect that LAI had on the modelled CO₂ fluxes was studied, since LAI is a very important factor in photosynthesis (Lindroth et al., 2008). The sensitivity analysis was performed using data from Hyytiälä in 2001. At Hyytiälä the LAI was 8 m²/m². The LAI was increased and decreased by 20%. First it was examined how the changes impacted the fluxes without re-parameterization of J_{\max} and $V_{c(\max)}$.

As LAI was decreased by 20%, the vegetation in lower layers obtained more light, yet the amount of assimilating biomass was decreased. This resulted in a lowering of the modelled CO₂ flux. On a bright summer day around noon

the modelled CO₂ flux maximum was 23% lower compared to the model result with the measured LAI. Next the re-parameterization was conducted by inversion; this caused an increase in both of the parameters. There was no other systematic change in the modelling results compared to the original model. However, more scattering was introduced, and on bright summer days the CO₂ flux was estimated to be up to 27% more than the model result with the original LAI.

When LAI was increased by 20%, the CO₂ flux was also systematically underestimated without re-parameterization, by approximately 9%. Even though there was more biomass, more attenuation of the incoming radiation occurred. A quarter of the biomass was located in the lowest layer, which was not receiving much light. After re-parameterization of J_{\max} , the model results were, on the average, close to the original ones. The highest difference between the two was approximately 14%.

Since similar summertime values for the parameters were obtained for different sites (Table 2), their applicability across the four sites was examined. Parameter values from Hyytiälä in summertime were applied to the other sites during summer. There is not much variation in the results for

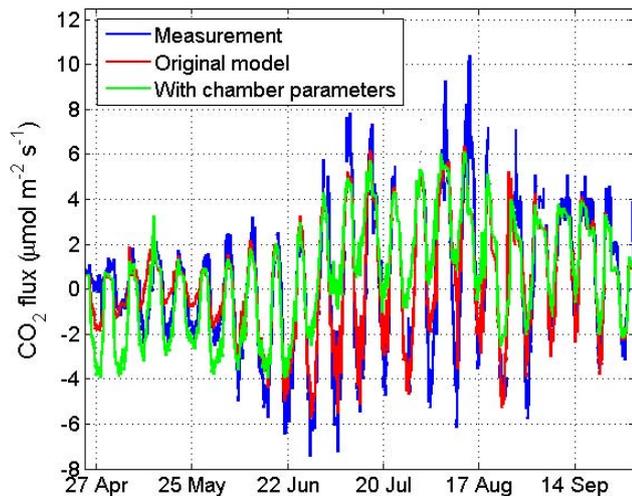


Fig. 3. The weekly averages for diurnal periods for the CO₂ flux measurements, the original model run and the model run with biochemical parameters estimated from chamber measurements (Aalto et al., 2002) at Sodankylä in 2001. Negative CO₂ fluxes denote uptake by vegetation and positive CO₂ fluxes respiration.

the summertime runs between the sites' own parameterization and Hyytiälä's values, r^2 (calculated from NEE) being between 0.53 and 0.78 (data not shown). Only at Sodankylä are the r^2 values were slightly smaller.

Since our estimations for the biochemical parameters, and especially for their relationship, differed from the values stated in the literature, they were examined more closely. Since their mutual relationship is considered to be relatively constant – 1.68 to 2.0 at 25°C (Medlyn et al., 2002b; Leuning, 2002), even though the magnitudes of the parameters may vary considerably, this was considered important. Also, in the Eq. (4) q is involved in the RuBP regeneration-limited rate, and controls the potential electron transport rate J . At low light levels, it is the parameter q that determines the RuBP-regeneration-limited rate, and therefore the lower light limit for estimating J_{\max} was set at $600 \mu\text{mol m}^{-2} \text{s}^{-1}$. Since q and J_{\max} appear in the same equation, their estimation might influence one another. When three parameters (J_{\max} , $V_{c(\max)}$, q) were optimized simultaneously, the light use efficiency q remained at a quite constant level of 0.14, same as in Aalto (1998). The new J_{\max} and $V_{c(\max)}$ values and corresponding fluxes were close to earlier estimates. This result gave us confidence in our previous estimates by inversion.

We used the parameterization made in Värriö for Scots pine using shoot chamber measurements (Aalto et al., 2002) and studied how the model performed with this parameterization (Fig. 3). The modelled fluxes were overestimated during April and May. During July and August the simulated fluxes greatly underestimated the measurements. In June and September the CO₂ fluxes were slightly underestimated by the model.

Table 3. Gross Primary Production (GPP), r^2 and index of agreement d at Sodankylä in 2001 with differently modified model simulations. “Original” refers to the model run with seasonally changing temperature dependencies, as presented in Table 2. Drought refers to atmospheric soil water stress.

	GPP (g C m ⁻²)	r^2	d
Original	190.1	0.71	0.91
One fit for parameters	173.7	0.61	0.86
Summertime fit only	223.1	0.66	0.90
Fixed base rate (f_0), variable E_f	182.0	0.69	0.90
Fixed E_f , variable base rate (f_0)	178.9	0.69	0.90
Dynamic LAI	185.4	0.69	0.90
Drought effect included	183.0	0.71	0.91

3.4 Effect of seasonality and atmospheric soil water stress on GPP

To study the significance of different seasonal fittings for the biochemical parameters and seasonally varying LAI and the effects of night frost and atmospheric soil water stress, we used Sodankylä data in 2001 as our test year and simulated GPP. To study the performance of the model we also calculated r^2 in respect to NEE and index of agreement d , that is suitable for eddy covariance data since it is not sensitive to outliers (Verbeeck et al., 2008). The index of agreement equals one in perfect agreement and lowers to zero in disagreement between observed and predicted values.

The effect of the seasonality included in the model via different temperature responses in spring and summer was investigated by simulation. When only the summertime temperature fits for the model parameters were employed throughout the year, the GPP increased by 17% from the original model run with seasonally changing temperature dependencies (Table 3). When one fit for each parameter for the whole year was done, GPP decreased 9% compared to the original one and the model performance was lowered.

To study the temperature sensitivity of the model we performed fittings of the activation energy (E_f) in Eq. (5) while keeping the base rate (f_0) fixed and vice versa. We did fittings for J_{\max} and $V_{c(\max)}$ for the same time periods used earlier at Sodankylä. For J_{\max} , E_f varied from 1.06×10^4 to $1.24 \times 10^4 \text{ J mol}^{-1}$ and f_0 from 194 to $267 \mu\text{mol m}^{-2} \text{s}^{-1}$ when the other was kept constant. For $V_{c(\max)}$ the parameter E_f varied from 6.58×10^4 to $9.89 \times 10^4 \text{ J mol}^{-1}$ and f_0 from 19.4 to $35.2 \mu\text{mol m}^{-2} \text{s}^{-1}$. Performing fittings of only f_0 or E_f lead to a decrease of 4–6% in GPP and did not have a large effect on the functioning of the model, accordingly on the r^2 and d (Table 3).

The night frosts lowered the values of the biochemical model parameters, as was seen in Fig. 2. We studied the possibility to take the night frost effect into account in our modelling. We took the spring time (1 May–3 June) inverted parameter values J_{\max} and $V_{c(\max)}$ at Sodankylä in

years 2001–2005 and tried to separate values that had experienced night frost on the previous night from the other values. There was not a clear difference seen in the temperature dependencies between these two groups. However, when the mean value of the parameters at temperature range 5–8°C was calculated, the values on days following night frosts had 30% lower mean value (both J_{\max} and $V_{c(\max)}$). The temperature responses used in this work did not clarify whether the effect of night frosts should be included in base rate or in activation energy or in both. We did a model simulation where the base rate of the both parameters was lowered by 30% after a night frost. This caused the spring time fluxes to be underestimated. The effect of this change on the annual GPP was less than 2%.

In the original model set-up the leaf area index (LAI) was kept constant throughout the year. We experimented how a seasonally varying LAI would influence our results. In northern Finland the needle biomass turnover rate of Scots pine is 0.10 (Muukkonen, 2005). At Sodankylä the new needles evolve from mid-June to mid-July and old needles fall down during August. We made a model run with LAI increasing evenly 10% from the basic value of 3.6 during mid-June to mid-July and decreasing in August. New parameterizations were performed for the biochemical model parameters using the same time periods as earlier. This change resulted in 3% drop in annual GPP and did not have large influence in performance of the model (Table 3).

To incorporate the effect of atmospheric soil water stress into the model, we used a similar approach as developed by Tuzet et al. (2003). The second term on the right hand side of the Ball-Berry equation (Eq. 6) was multiplied by a coefficient. This coefficient was a sigmoid function which decreased as a function of increasing VPD. This same method has earlier been shown to succeed at Sodankylä by Thum et al. (2007). New parameterization for the biochemical model parameters was not performed since the added atmospheric soil water stress effect did not largely change their values. Taking atmospheric soil water stress into account resulted in 4% lowering of GPP and it did not influence the functioning of the model.

4 Discussion

4.1 The magnitude of the biochemical model parameters

The values of the biochemical parameters (J_{\max} and $V_{c(\max)}$) were comparable at all sites, the parameterizations performed for the different sites yielded surprisingly similar results. The parameterizations obtained were also applicable for other years at each site. More importantly they were suitable for all four sites during the summertime. Originally, more variation in the results with latitude and different species was expected. However, according to Bergeron

et al. (2007), there was not much variability in three boreal black spruce forests located in different climatic zones regarding the temperature responses of gross ecosystem production and respiration on a monthly timescale. Medlyn et al. (2005a) studied three different coniferous sites and found that the largest difference in net ecosystem productivity was caused by soil respiration, with needle respiration also playing a role.

The results for Scots pine forest in Sodankylä were compared to literature in Thum et al. (2007). The J_{\max} values were in quite good accordance at low temperatures with the literature but highly exaggerated at temperatures above 15°C. The $V_{c(\max)}$ values were close to the literature values. The same applies to the two more southern Scots pine sites. For Sodankylä $J_{\max, \text{std}}$ at 17°C was $193.8 \mu\text{mol m}^{-2} \text{s}^{-1}$, Hyytiälä $J_{\max, \text{std}}$ was $153.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ and in Norunda $170.1 \mu\text{mol m}^{-2} \text{s}^{-1}$, as shown in Table 1 and multiplied by π in order to convert from total leaf area to the projected leaf area (Stenberg et al., 1995). For $V_{c(\max), \text{std}}$ we had $49.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ in Sodankylä, $32.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ in Hyytiälä and $35.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ in Norunda. The literature values for the biochemical parameters are shown in Table 4.

In the literature (Wullschleger, 1993), there is a difference between the parameter values for Norway spruce and Scots pine, the latter giving considerably higher estimates. For Norway spruce, Wullschleger (1993) has given two estimates from two different measurements, shown in Table 4, measured at higher temperatures than ours. In this inversion for Kenttäröva we estimated $J_{\max, \text{std}}$ to be $161.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ during summer time at 17°C. For $V_{c(\max), \text{std}}$ we obtained $33.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ during summer. Compared to the biochemical parameters measured by Grassi et al. (2001) our $J_{\max, \text{std}}$ value was large and our $V_{c(\max), \text{std}}$ estimation was on the same scale (Table 4). Estimates for Flakaliden in Sweden are of the same magnitude (Robertz and Stockfors, 1998).

The values are shown for 17°C, since this is a common summertime temperature in northern Finland. Usually the values of biochemical model parameters are given for 25°C, but since this is an uncommon temperature at many of the sites, it was not possible to make a reliable fitting in that temperature range. From leaf chamber measurements in northern Finland at Värriö it was only possible to estimate the parameter J_{\max} below 20°C (Aalto, 1998). In estimations of J_{\max} in Finland, the fitted temperature response has been found to have an optimum: in Aalto (1998) the optimum J_{\max} value was below 20°C and in Wang et al. (1996) the optimum was below 25°C. Our obtained temperature dependencies of the parameters show no optimum value in the studied temperature range and thus it is in agreement with more generalized studies in this subject (Hikosaka et al., 2006; Kattge and Knorr, 2007).

According to the literature, the biochemical model parameters are considered to have a relatively constant ratio to each other, the relation $J_{\max}/V_{c(\max)}$ usually being around 1.68 to 2.0 (Medlyn et al., 2002b; Leuning 2002) at 25°C. Since the

Table 4. Literature values for the biochemical model parameters.

Species	J_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	$V_{c(\max)}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Temperature ($^{\circ}\text{C}$)	Reference
Scots Pine	121	46	17	Wullschleger (1993)
	95.7	44.8	17	Aalto et al. (2002)
	118	60.3	17	Wang et al. (1996)
	314.9	121.9	25	Medlyn et al. (1999)
Norway Spruce	32	12	20	Wullschleger (1993)
	17	6	24	Wullschleger (1993)
	57.8	23.4	25	Grassi et al. (2001)
	63	37	19	Roberntz and Stockfors (1998)

temperature dependencies of J_{\max} and $V_{c(\max)}$ are dissimilar this ratio is dependent on temperature: at 20°C their ratio has been estimated to be 2.68 (Leuning, 1997). In our measurements the relationship between the two biochemical parameters was not as represented in the literature: J_{\max} had larger values at higher temperatures. At standard temperature (17 °C) the ratio $J_{\max,\text{std}}/V_{c(\max),\text{std}}$ during summertime varied between 3.9 and 4.9 at different sites. This caused the model to function poorly when using literature values for the parameters, but with our own estimates it worked as expected. However, in the literature it has also been suggested that the ratio might be influenced by growth temperatures (Kattge and Knorr, 2007) and that the ratio is affected by seasonality (Xu and Baldocchi, 2003). Often in literature the ratio is kept constant and only $V_{c(\max)}$ is optimised (Wang et al., 2006; Verbeeck et al., 2006). Seasonal variation in the ratio might thus be neglected (Verbeeck et al., 2008).

4.2 Seasonality of the biochemical model parameters

The springtime temperature dependencies were at a lower level at all sites. At Hyytiälä it was found possible to obtain more temperature responses for the parameters than at the other sites. This might be due to the more extensive time series or to some influence by the deciduous trees on the site. At Hyytiälä the model performed better with separate fits e.g. for $V_{c(\max)}$ in April and May.

The seasonality of the parameters has been observed in many deciduous species (Wilson et al., 2001; Xu and Baldocchi 2003; Kosugi et al., 2003) and also in evergreen broadleaf species (Kosugi and Matsuo, 2006). In a similar eddy flux data inversion as in this study done by Wang et al. (2006), no seasonality in the biochemical parameters of the conifer forests was observed, even though Hyytiälä was one of the sites studied. The seasonality of the biochemical model parameters in conifer forests has been observed in some measurements (Rayment et al., 2002; Medlyn et al., 2002a; Han et al., 2004).

The role of the night frosts in delaying the spring recovery has been shown earlier (Ensminger et al., 2004; Bergh and Linder, 1999), recently also the importance of the cold soil temperatures has been brought up (Ensminger et al., 2008). Changes occurred in the temperature responses of the parameters in spring. We studied whether changes in the parameters are due to differences in the photosynthetic capacity ($J_{\max,\text{std}}$ and $V_{c(\max),\text{std}}$) or the temperature dependencies of the parameters. We fitted the temperature response functions differently, by having base rate or activation energy as constant throughout the year while the other one was fitted. The changes in both activation energy and base rate were larger for $V_{c(\max)}$ than for J_{\max} . When the base rate was fixed, the activation energy of $V_{c(\max)}$ varied by 34%. When the activation energy was fixed, the base rate of $V_{c(\max)}$ varied by 45%. Thus, no clear difference was seen in the range of variation of activation energy and base rate due to seasonality. Since our fitting periods were long, it was not straightforward to separate whether air temperature was coupled to photosynthetic capacity $J_{\max,\text{std}}$ and $V_{c(\max),\text{std}}$ or the temperature dependencies of the parameters.

In a study by Kosugi and Matsuo (2006) parameter $V_{c(\max),\text{std}}$ and its temperature dependency was studied by leaf gas exchange measurements in evergreen trees in western Japan. Only changes in $V_{c(\max),\text{std}}$ were found. It is possible that different temperature dependencies in spring originate only from changes in photosynthetic capacity.

The effect of seasonally changing LAI might also influence our results. We studied this at Sodankylä and there its influence was small. The effect might be larger at Hyytiälä, since the needle turnover rate is larger in southern Finland (0.21) than in northern Finland (0.10) (Muukkonen, 2005). There are some deciduous trees in the footprint of the Hyytiälä eddy covariance measurement, their percentage being anyhow small. Since we did not have data on their effect, we did not study the sensitivity of the model to seasonally varying LAI at Hyytiälä. The atmospheric soil water stress effect in summertime was studied, since it might have effect on the seasonal behaviour seen in the parameters. At Sodankylä this influence was small.

According to the simulation runs, the effect of seasonality via the different temperature responses of the model parameters has a quite remarkable effect on GPP. Modelling the seasonality is still a challenge for vegetation models today (Sasai et al., 2007; Ricciuto et al., 2008; Harrison et al., 2008).

4.3 Modelling assumptions

Inversion modelling was used in the parameterizations. Many different factors might thus influence these results. The estimated parameters are obtained by using eddy covariance measurements and not all processes occurring at the canopy level have been perfectly described. These include e.g. radiative transfer, conductance module and description of respiration. Also, many of the model parameters were kept constant during optimization process and different needle age classes were not accounted for. In some models needle age classes are considered important (Ogée et al., 2003) but we did not have enough measurements to model them. All of these effects might provide reasons why our ratio between J_{\max} and $V_{c(\max)}$ as well as some other results differed when compared to the literature. However, since the same method was used at all sites, the similar summertime results indicate suitability of the same biochemical parameters in these forests.

Estimating respiration from the night-time eddy flux measurements was also an error source (Reichstein et al., 2005). Using only air temperature and not soil temperature at three sites for soil respiration might lead to biased respiration estimates during snow melt, when soil temperature is constantly at zero degrees (Arneeth et al., 2006). However, air temperature explains more of the variance in the ecosystem respiration and measurements of soil temperature at 5–10 cm depth might not describe fully the respiration process that is partly occurring in the uppermost soil layer (Reichstein et al., 2005). According to our needle chamber measurements the needle respiration was exponential in the ambient temperature range at Sodankylä and thus using exponential function for needle respiration was justified. Needle respiration might be limited by carbohydrates on seasonal timescales but this was not noticed in our needle chamber measurements done at Sodankylä from spring to summer in 2002.

We divided the biochemical model with simple upscaling into small parts in order to obtain values for the model parameters. The more complicated models do not necessarily outstand the simpler ones (Lawrie and Hearne, 2007). There are e.g. models based on light use efficiency that yield very good estimations for GPP (Mäkelä et al., 2008) and they often provide better results than process-based models (Moffat et al., 2007). These models are not however useful for scenario runs since increase of CO₂ is not included in them (Verbeeck et al., 2008). Therefore simple models using the biochemical approach are useful.

5 Conclusions

We studied four different forest stands in the boreal zone and obtained estimates of the seasonality in the biochemical parameters via inverse modelling using eddy covariance data. For the biochemical model parameter J_{\max} we were able to acquire spring and summertime temperature responses separately for all the sites except for Norunda, for which we got only a summertime temperature dependency. The springtime temperature responses were at a lower level and did not increase as strongly with temperature as the summertime temperature dependencies. For the biochemical model parameter $V_{c(\max)}$, we were able to obtain both springtime and summertime temperature responses for all the sites. At Hyytiälä and Sodankylä it was even possible to describe the spring recovery in two phases. Hyytiälä also had a separate temperature dependency for $V_{c(\max)}$ during the autumn-time. The summertime parameterizations for Hyytiälä were applicable at all sites. Our estimation method by using eddy covariance data enables using data from cold spring period, which is often left unmeasured with leaf chambers.

With the help of temperature indices, better modelling results can be attained by binding the changeover dates of the parameters' temperature fits to temperature. The temperature sum is useful in this context, as is also the five-day average temperature, on condition that it is uniquely defined.

In the future, the warming of the climate will be more pronounced in higher latitudes (Trenberth et al., 2007) and will thus affect the boreal forests, that play an essential role in the global carbon balance (Schulze, 2006). Studying the behaviour of the boreal forests facing this warming is thus of the utmost importance.

Larger-scale parameterizations are needed for the models, and phenomenology is important for assessing the carbon balances of the northern areas. It is possible to use this model to study the future climate, since the model includes CO₂ concentration and seasonality of the model parameters is connected to the air temperature. However, not all the model assumptions will be valid in the future climate. An increase of temperature might lead to some acclimation of the biochemical model parameters (Kattge and Knorr, 2007; Way and Sage, 2008), so it is not obvious that we can use our parameterization as it is. An enhancement of CO₂ concentration has been reported to cause changes in the anatomy and photosynthetic capacity of the Scots pine needles (Luomala et al., 2003; Luomala et al., 2005), as well as changes in stomatal conductance in plants (Ainsworth and Rogers, 2007). An increase in the ambient CO₂ concentration might also change feedbacks from the vegetation (Janssens et al., 2005) and e.g. frost hardiness (Repo et al., 1996). In order to get an insight into the carbon balances of forests in the future, also knowledge of the respiration fluxes and their seasonal behaviour is essential (Law et al., 2002; Falge et al., 2002; Medlyn et al., 2005a).

Modelling measured eddy covariance fluxes contains many sources of uncertainties (Medlyn et al., 2005b; Rannik et al., 2006) but inverse modelling of these fluxes can be used to obtain important results (Reichstein et al., 2003) and eddy covariance measurements can be used in model parameterization (Hollinger et al., 2004; Verbeeck et al., 2008). It was interesting to notice that in this study we can obtain seasonally-resolved temperature responses for biochemical parameters if we have an extensive enough dataset, as we had at Hyttiälä. We were also able to capture the decrease in the photosynthetic capacity during autumn, as has been observed in e.g. Repo et al. (2006).

Our model was sensitive to changes in the leaf area index on daily scale, not on annual time scale. As the LAI was changed, the radiative transfer and description of the forest stand played a significant role. It was therefore not straightforward to separate the various effects. It would be good to implement various different radiative transfer models throughout the whole model and investigate their impact on the modelling results.

To study further how the parameters $J_{\max, \text{std}}$ and $V_{c(\max), \text{std}}$ change in spring, measurements made at Sodankylä could be used. Amount of parameter values obtained from inversion could be increased by adding latent heat flux into the model, thus also afternoon measurements could be used. Maximum photochemical efficiency Fv/Fm has been measured at Sodankylä since spring 2001. Comparing Fv/Fm to $J_{\max, \text{std}}$ and $V_{c(\max), \text{std}}$ could show whether only the photosynthetic capacity is changing or also the temperature dependencies of the parameters.

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