

*Biogeosciences Discussions* is the access reviewed discussion forum of *Biogeosciences*

# Assessing seasonality of boreal coniferous forest CO<sub>2</sub> exchange by estimating biochemical model parameters from micrometeorological flux observations

T. Thum<sup>1</sup>, T. Aalto<sup>1</sup>, T. Laurila<sup>1</sup>, M. Aurela<sup>1</sup>, A. Lindroth<sup>2</sup>, and T. Vesala<sup>3</sup>

<sup>1</sup>Finnish Meteorological Institute, Global and Climate Change Research, P.O. Box 503, FI-00101 Helsinki, Finland

<sup>2</sup>Lund University, Department of Physical Geography and Ecosystems Analysis, Sölvegatan 12, S-223 62, Lund, Sweden

<sup>3</sup>University of Helsinki, Department of Physics, P.O. Box 64, FI-00014 University of Helsinki, Finland

Received: 29 May 2008 – Accepted: 29 May 2008 – Published: 27 June 2008

Correspondence to: T. Thum (tea.thum@fmi.fi)

Published by Copernicus Publications on behalf of the European Geosciences Union.

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Abstract

The biochemical seasonality 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  $17^\circ\text{C}$ . The sensitivity of the model to LAI was also studied. Simulation runs were done to study the effect of the seasonality implemented in the model using different temperature fits. The impact of seasonality on annual GPP was 15%, which corresponded to an increase of  $2^\circ\text{C}$  in air temperature.

## 1 Introduction

According to scenarios of future climate, the boreal forest zone is expected to experience 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 assessed this by investigating boreal sites at different latitudes and comparing them.

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-

**BGD**

5, 2707–2747, 2008

## Seasonality of boreal coniferous forest $\text{CO}_2$ exchange

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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, and therefore it is essential to also do parameterization of 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 three important parameters: the maximum carboxylation rate ( $V_{c(max)}$ ), the maximum potential electron transport rate ( $J_{max}$ ) and the efficiency factor for the use of light ( $q$ ). 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 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 temperatures are 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 CO<sub>2</sub> flux observations by inverting a

---

**Seasonality of boreal coniferous forest CO<sub>2</sub> exchange**T. Thum et al.

---

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

canopy photosynthesis model. Our motivation was to study whether the phenomenology of larger-scale models can be improved, and also to assess how a warmer climate will affect the carbon balances of northern boreal forests.

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 the three biochemical model parameters were assessed, as well as the relations between air temperature and the biochemical model parameters, over the whole growing season. Also, it was investigated whether temperature indices could be used in improving the seasonality of the biochemical parameters in the modelling. In addition, the effect of night frosts was studied at different sites together with how its effect on the delay in the spring recovery was different for different values of the temperature sum. Finally, some simulation runs were conducted in order to study how large an impact the modelled seasonality and future climate conditions will have on GPP.

## 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 ( $67^{\circ}59'N$ ,  $24^{\circ}15'E$ ) and Sodankylä ( $67^{\circ}21'N$ ,  $26^{\circ}38'E$ ), are situated in northern Finland and in the northern boreal zone (Solantie, 2005). The Sodankylä site is a Scots pine (*Pinus Sylvestris*) forest (total Leaf Area Index, LAI 3.6). Kenttäröva is a homogenous Norway spruce (*Picea abies*) forest (LAI 6.6). The Scots pine-dominated forest at Hyytiälä ( $61^{\circ}51'N$ ,  $24^{\circ}17'E$ , LAI 8.0) is in the southern boreal zone in Finland. The southernmost site of Norunda ( $60^{\circ}50'N$ ,  $17^{\circ}28'E$ ) is in the hemi-boreal zone in the central part of Sweden. Norunda is a mixed Scots pine/Norway spruce coniferous forest (LAI 13.5). Annual mean temperatures range from  $-1.7^{\circ}C$  in the northern boreal

**BGD**

5, 2707–2747, 2008

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



zone to 5.5°C in the hemi-boreal zone. More detailed descriptions of the sites are to be found in Lindroth et al. (2008).

We used at least two years of data from each of these sites: Hyytiälä 2000–2001, Sodankylä 2001–2004 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. The global radiation and reflected radiation were used to calculate albedo.

## 2.2 Modelling and data analysis

A canopy-level gas exchange model was parameterized by inversion from the canopy CO<sub>2</sub> flux data. The leaf level CO<sub>2</sub> 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.

$A_j$  -assimilation is

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

and  $A_c$  -assimilation is described as

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

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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 CO<sub>2</sub> and O<sub>2</sub>,  $\Gamma^*$  is the CO<sub>2</sub> 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 that is a function of incident irradiance, the light use efficiency factor ( $q$ ), the convexity of the light response curve and  $J_{\max}$ , the maximum rate of electron transport.

The temperature dependence of  $\Gamma_*$  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).  $V_{c(\max)}$  and  $J_{\max}$  have an Arrhenius-type temperature dependency (Harley and Baldocchi, 1995):

$$f_T = f_0 \exp \left[ \frac{E_f(T - 298.15)}{298.15RT} \right] \quad (3)$$

where  $f_0$  denotes the parameter ( $V_{c(\max),o}$  or  $J_{\max,o}$ ),  $E_f$  is the activation energy,  $R$  is the gas constant and  $T$  is temperature in Kelvin.

The Ball-Berry conductance (Ball et al., 1987) was used in conjunction with the biochemical model for describing the stomatal 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).

Before we can use NEE data from eddy covariance measurements for calculation of photosynthesis parameters, we have to subtract the respiration components.

---

**Seasonality of boreal  
coniferous forest CO<sub>2</sub>  
exchange**T. Thum et al.

---

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

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. The fittings were made to biweekly data sets, and both of the two parameters (respiration at 10°C and the activation energy) were fitted. 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.

The soil and needle respiration dependencies on temperature and the vertical biomass distribution were 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).

A parameterization year was chosen, and temperature responses for the biochemical model parameters  $J_{\max}$  and  $V_{c(\max)}$  were obtained from the inversed CO<sub>2</sub> flux data. For estimating the biochemical parameters, a procedure introduced by Lloyd et al. (1995) was used: The measured CO<sub>2</sub> 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. Inversed parameter values were plotted as a function of temperature, and Arrhenius-type fittings (Eq. 3) were performed. Further details of the optimization process are presented in Thum et al. (2007).

---

**Seasonality of boreal  
coniferous forest CO<sub>2</sub>  
exchange**T. Thum et al.

---

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

The biochemical model parameters were solved by inversion for all the years studied, and daily averaged values of them were used in conjunction with the values of the temperature-related indices to study the seasonality of the different forests. To study whether parameterizations are also applicable during other years, model runs for different years were done. In these runs, various different temperature responses were temporally kept the same as they were in the parameterization year. The applicability of the summertime parameterization at Hyytiälä to other sites was investigated.

We also improved the modelling of seasonality by using temperature indices. 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. The spring recovery of forests is more dependent on temperature than on the calendar date. Moving these 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 floating average temperature (Tanja et al., 2003).

Simulation runs were conducted for one year at Sodankylä. We compared the control run GPP having realistic Sodankylä data with model runs separately as follows: without seasonality, with a doubled CO<sub>2</sub> concentration, with a two-degrees warmer temperature and with both of the last two effects combined.

We studied the sensitivity of the inversed model parameters to the LAI, since LAI is very important factor in photosynthesis (Lindroth et al., 2008). The effect of LAI on the modelling results was investigated by changing its value in 2001 at Hyytiälä by 20%. We also studied the functioning of the model with other values of the biochemical parameters. In fact, there are three important parameters involved: as well as the above-mentioned  $J_{\max}$  and  $V_{c(\max)}$ , the internal light use efficiency  $q$  also plays an important part in the model. In many models it is  $V_{c(\max)}$  and  $q$  that are estimated, while  $J_{\max}$  is just assumed to have a certain relationship to  $V_{c(\max)}$  (Wang et al., 2003; Verbeeck et al., 2006).



In the Eq. (1)  $q$  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. In order to study this possibility, we simultaneously minimized all three biochemical parameters for Hyytiälä, and looked at what effect this had on their values.

We also assumed a constant relationship between  $J_{\max}$  and  $V_{C(\max)}$ , using the equation

$$J_{\max} = 29.1 \mu\text{mol m}^{-2} \text{s}^{-1} + 1.64 V_{C(\max)} \quad (4)$$

from Wullschleger (1993) and estimated  $J_{\max}$  with this equation from the inversed  $V_{C(\max)}$  values. In this examination  $q$  was kept constant. We looked at the ratio of the two parameters with this kind of estimation. In addition to these values, we studied the performance of the model with  $J_{\max}$  and  $V_{C(\max)}$  taken from shoot chamber measurements made at Värriö, which is located in Finnish Lapland (Aalto et al., 2002).

## 3 Results

### 3.1 The parameterization at different sites

We obtained plots for temperature dependencies from model inversion. 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.

**BGD**

5, 2707–2747, 2008

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Seasonality of boreal  
coniferous forest CO<sub>2</sub>  
exchange**

T. Thum et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

The fitting parameters are shown in Table 1 together with the values of the biochemical parameters at 17°C. In the summertime fits, the values for  $J_{\max}$  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  $V_{c(\max)}$  at 17°C 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. In all the figures the temperature responses were extrapolated for the temperature range shown in the figure, even though the temperature for the springtime dependencies did not cover this whole range. 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. 2a and b. 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 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. 3. 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 the 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 points were quite scattered (Fig. 4). 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.

Model runs for different years were conducted. In Table 2,  $r^2$  values are shown for the model performance during the whole growing season in the various years studied. The model also succeeded similarly in those years that were not used for the parameterization. Since similar summertime values for the parameters were obtained (Table 1), their applicability across the four sites was examined. Parameter values from Hyytiälä in summertime were applied to the other sites during summer. The  $r^2$  values from these simulations are also shown in Table 2. There is not much variation in the results for the summertime runs between the sites' own parameterization and Hyytiälä's values. Only at Sodankylä are the  $r^2$  values then slightly smaller.

### 3.2 Linking seasonality to temperature indices and modelling

In Fig. 5a the daily values of the inverted biochemical parameters  $J_{\max}$  and  $V_{c(\max)}$  for Kenttäröva in the year 2001 are shown. The CO<sub>2</sub> flux measured by eddy covariance method is shown in Fig. 5b. The five-day floating average temperature (5Dave) the minimum temperature are also shown (Fig. 5c). The same parameters, data and five-day average temperature for Sodankylä, Hyytiälä and Norunda, respectively in Figs. 6–8 are represented. For the biochemical parameters similar values were obtained at all the sites. At Norunda and Hyytiälä. the first night frost of the autumn caused a large drop in the biochemical parameters (Figs. 7a and 8a).

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



---

**Seasonality of boreal  
coniferous forest CO<sub>2</sub>  
exchange**T. Thum et al.

---

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

We investigated the relation between the temperature sum and the inversed biochemical model parameters. The temperature sum is defined as the sum of positive daily average temperatures. At Hyytiälä it was observed that, when the temperature sum was below 270°C d, night frosts resulted in a lowering of  $V_{c(max)}$  to early springtime values. Later-occurring night frosts did not have such large effect, only causing some reduction in the rate of increase of  $V_{c(max)}$ . At Norunda similar behaviour was found. The temperature sum rose above 270°C d during mid-May at Hyytiälä and during late April–early May at Norunda.

At the Sodankylä and Kenttäröva sites, severe night frosts occurred until the end of May. At such northern sites some night frosts may even take place during August, as happened at Sodankylä during 2001 and 2004. When the temperature sum was below 200°C d, the night frosts seemed to have some effect on the biochemical parameters at these two sites. Crossing this threshold occurred during late May–early June in both places.

As a result of the optimizations the sites obtained several temperature responses for the biochemical parameters, as was seen in Figs. 1–4. 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 CO<sub>2</sub> fluxes.

We used 2002 at Sodankylä and 2000 at Hyytiälä as our test years. The five-day running temperature and the temperature sum were used to as proxies to describe the photosynthetic state of the vegetation (Tanja et al., 2003).

The changeover dates of the temperature responses of the parameterization year 2001 in Sodankylä were 4 June and 25 June. Taking the temperature sums on these two days and locating them in the year 2002 resulted in the dates 27 May and 12 June.

When the model was run with these new changeover dates, the modelling results were improved.

Using the five-day running temperature it was feasible to locate the first changeover date, which was 29 May, but it was not possible to define the other date. The temperature limit was crossed many times. This occurred for the first time on 30 May; trying this as the second changeover date caused overestimation of the fluxes. Using May 29 as the first changeover date did improve modelling results, however.

At Hyytiälä there were three changeover dates, two of them taking place during spring time. The first changeover date for temperature dependencies in the parameterization year 2001 was May 1 and the second 1 June. With the temperature sum, the corresponding dates in 2000 were 27 April and 25 May. Applying these dates for changing the temperature responses yielded better modelling results. At Hyytiälä there was also a separate fitting period for the autumn time starting, in 2001, on 1 September. The temperature sum approximated the corresponding change to be on 6 September in 2000. It was not possible to see if using this new date improved modelling results because there was a data gap in the flux measurements at this time.

The five-day running average temperature estimated the first changeover date in spring 2000 to be 21 April. This approximation gave even better results than the earlier estimate by the temperature sum. It was not possible to obtain the second changeover date because that temperature limit was crossed many times. During autumn the estimation was taken from the last crossing of the temperature limit (12.3°C), on 3 September. Again, it was not possible to compare the modelling results due to the data gap, but it was interesting that the two methods gave estimates for the changeover date in autumn that were very close to each other.

### 3.3 Effect of climate warming and seasonality in the simulation experiments

A control run was performed using realistic data for one year at Sodankylä. The GPP for the control run was 190.1 g C m<sup>-2</sup>. In the first experiment the CO<sub>2</sub> concentration was doubled. This caused an increase of 20% in GPP. In the second experiment the

---

**Seasonality of boreal coniferous forest CO<sub>2</sub> exchange**

T. Thum et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



temperature was raised by two degrees. The dates for the switching of the temperature fits was made according to the method described in the previous section, using the temperature sum. The GPP was calculated with temperature fits for the biochemical model parameters levelling off at 20°C and also with temperature fits continuing to increase after this point. The first approach gave a 13% addition to GPP and the latter a 16% increment. The last experiment included increases in both temperature and CO<sub>2</sub> concentration. Without the upper threshold for temperature fits for the model parameters there was a 41% addition to GPP, while with the limiting conditions the increment was 37%.

The effect of the seasonality included in the model via different temperature responses in spring and summer was also investigated by simulation. When only the summer time temperature fits for the model parameters were employed throughout the year, the GPP increased by 15%.

### 3.4 Sensitivity analysis

#### 3.4.1 Effect of LAI

In the sensitivity analysis, the effect that LAI had on the modelled CO<sub>2</sub> fluxes was studied. The sensitivity analysis was performed using data from Hyytiälä in 2001. At Hyytiälä the LAI was 8 m<sup>2</sup>/m<sup>2</sup>. The LAI was increased and decreased by 20%. First 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 CO<sub>2</sub> flux. On a bright summer day around noon the modelled CO<sub>2</sub> 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

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



bright summer days the  $\text{CO}_2$  flux was estimated to be up to 27% more than the model result with the original LAI.

When LAI was increased by 20%, the  $\text{CO}_2$  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%.

### 3.4.2 Different ways to estimate $J_{\max}$

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 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).

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, even though the magnitudes of the parameters may vary considerably, this was considered important. 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. This was the same value as that estimated earlier based on the literature values (Aalto, 1998). The new  $J_{\max}$  and  $V_{c(\max)}$  values were close to earlier estimates. This result gave us confidence in our previous estimates by inversion.

Closer inspection of the inversed  $J_{\max}$  values led to the conclusion that the  $A_j$  and  $A_c$  – limited rates were alternating as was expected. The  $A_c$  – limited rate was dominant in very good light conditions, while photosynthesis was limited by  $A_j$  at lower light levels.

We used Eq. (4) (Wullschlegel, 1993) to estimate  $J_{\max}$  at Hyytiälä in 2001. The new  $J_{\max}$  values are shown in Fig. 9a. Here we have the values for  $J_{\max}$  that were obtained,

## Seasonality of boreal coniferous forest $\text{CO}_2$ exchange

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



when  $V_{c(\max)}$  was optimized and  $J_{\max}$  was then estimated by Eq. (4). When compared to the inversed results displayed in Fig. 3a, it was noticed that, at temperatures above 15°C, these two different approaches gave values of the same magnitude. At lower temperatures the difference was more pronounced. At around 10°C, Eq. (4) gave values in the range 35 to 40  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , whereas our inversion results were around 18 to 24  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Equation (4) is based on results at temperatures at which the  $A/C_i$ -curves used in the parameterization were measured; these results do not include any measurements at temperatures below 20°C (Wullschlegler, 1993).

Equation (4) is based on the relationship between  $J_{\max}$  and  $V_{c(\max)}$  of 109 plant species. From our inversion we obtained the value of 10.4  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for  $V_{c(\max)}$  at 17°C at Hyytiälä. By inversion we got 48.8  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for  $J_{\max}$ . Placing the Hyytiälä value for  $V_{c(\max)}$  in Eq. (4) produced 46.2  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , which is close to our inversed estimation. This led to a ratio 4.4 between the parameters, however, which is different from that found in the literature.

We studied three different methods to estimate the parameters. In the first approach, the inversed  $V_{c(\max)}$  values were used, and  $J_{\max}$  was estimated using Eq. (4). In the second approach, we used the parameterization made in Värriö for Scots pine using shoot chamber measurements (Aalto et al., 2002). The third approach was the inversion modelling of the eddy covariance data for both of the parameters. Three different temperature relationships for  $J_{\max}$  are displayed in Fig. 9a), i.e., our summertime estimate from the inversion, Eq. (4) results and the fit obtained from chamber measurements. In Fig. 9b) the fits from inversion and chamber measurements for  $V_{c(\max)}$  are shown.

When we used parameter values from the chamber measurements, the modelled fluxes were greatly overestimated during April and May. During the summer months the simulated fluxes underestimated the measurements. In September and October the  $\text{CO}_2$  fluxes were slightly exaggerated by the model. This behaviour can be seen from the temperature fits in Fig. 9. At low temperatures the fit from the chamber is higher than the fits from the EC measurements, especially during the spring months,

## Seasonality of boreal coniferous forest $\text{CO}_2$ exchange

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





whose fits are shown in Fig. 3. At higher temperatures the fit is lower than the inverted fit, and as a result the warm days are underestimated.

Using the estimation for  $J_{\max}$  from Eq. (4) resulted in similar results to the inverted  $J_{\max}$ , except that during April the simulated flux is overestimated. This was caused by the difference in the estimations of  $J_{\max}$  at low temperatures.

## 4 Discussion

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 (Table 1). 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.

When comparing our values to the literature, we need to multiply our parameters by  $\pi$ , in order to convert from total leaf area to the projected leaf area (Stenberg et al., 1995).

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 in low temperatures with the literature but highly exaggerated in 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  $J_{\max}$  in 17°C was  $193.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ , Hyytiälä  $J_{\max}$  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  $\pi$ . For  $V_{c(\max)}$  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 3.

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The values in Table 1 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.

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 3, measured at higher temperatures than ours. In this inversion for Kenttäröva we estimated  $J_{\max}$  to be  $161.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  during summer time at 17°C. For  $V_{C(\max)}$  we obtained  $33.0 \mu\text{mol m}^{-2} \text{s}^{-1}$  during summer. The literature values are shown in Table 3. Compared to the biochemical parameters measured by Grassi et al. (2001) our  $J_{\max}$  value was large and our  $V_{C(\max)}$  estimation was on the same scale. Estimates for Flakaliden in Sweden are of the same magnitude (Roberntz and Stockfors, 1998).

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.

**Seasonality of boreal coniferous forest CO<sub>2</sub> exchange**

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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 relationship between the two biochemical parameters was not as represented in the literature: in our measurements  $J_{\max}$  had larger values at higher temperatures. 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). Modelling the seasonality is still a challenge for vegetation models today (Sasai et al., 2007; Ricciuto et al., 2008; Harrison et al., 2008).

The parameterizations obtained were also applicable for other years at each site. More importantly they were suitable for all four sites during the summertime. Inversion modelling was used in the parameterizations. Many different factors might thus influence these results, e.g. the descriptions of respiration, radiative transfer and the conductance module. These might provide reasons why our ratio between  $J_{\max}$  and  $V_{c(\max)}$  as well as certain other of our 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.

In order to get an insight into the carbon balances of forests in the future, knowledge of the respiration fluxes and their seasonal behaviour is essential (Law et al., 2002; Falge et al., 2002; Medlyn et al., 2005a). Since our modelling contained only a rough estimate of the respiration, we can only discuss the photosynthesis side in more detail.

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.,

**Seasonality of boreal coniferous forest CO<sub>2</sub> exchange**

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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 CO<sub>2</sub> is not included in them (Verbeeck et al., 2008). Therefore simple models using the biochemical approach are useful.

5 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. Incrementing both temperature and CO<sub>2</sub> concentration enhances GPP. It is not a straightforward matter, however, that the model assumptions will hold in the actual conditions of the scenarios. An increase of temperature might lead to some acclimation of the  
10 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 CO<sub>2</sub> 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). However, Bernacchi et al. (2006) and Leakey et al. (2006) suggest that the effects of CO<sub>2</sub>  
15 concentration increase have been overestimated.

## 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  
20 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  
25 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

---

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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.

5 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.

10 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. In our simulation runs we noticed that the relative change in GPP due to seasonality was as large as the impact of a 2°C increase in air temperature. The increment of GPP was also larger with increases in both temperature and CO<sub>2</sub> concentration together than as the sum of their influences calculated separately.

20 In the future climate the role of respiration will also be important, but this was not assessed in this study. An increase in the ambient CO<sub>2</sub> concentration might also change feedbacks from the vegetation (Janssens et al., 2005) and e.g. frost hardness (Repo et al., 1996).

25 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 Hyytiälä. We were also able to capture the decrease

---

**Seasonality of boreal coniferous forest CO<sub>2</sub> exchange**T. Thum et al.

---

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

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. 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.

*Acknowledgements.* We gratefully acknowledge the financial support from the Academy of Finland, the Nordic Council of Ministers, the European Commission and the Maj and Tor Nessling Foundation. Many thanks are also due to the personnel of the measurement sites.

## References

Aalto, T.: Carbon dioxide exchange of Scots pine shoots as estimated by a biochemical model and cuvette field measurements, *Silva Fenn.*, 32, 321–337, 1998.

Aalto, T., Hari, P. and Vesala, T.: Comparison of an optimal stomatal regulation model and a biochemical model in explaining CO<sub>2</sub> exchange in field conditions, *Silva Fenn.*, 36, 615–623, 2002.

Ainsworth, E. A. and Rogers, A.: The response of photosynthesis and stomatal conductance to rising [CO<sub>2</sub>]: mechanisms and environmental interactions, *Plant, Cell and Environ.*, 30, 258–270, 2007.

Ball, J. T., Woodrow, I. E., and Berry, J. A.: A model for predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions, in: I. Biggins (Ed.), *Progress in photosynthesis research*, Vol IV. Martinus Nijhoff Publishers, Netherlands, pp. 221–224, 1987.

Bergeron, O., Margolis, H. A., Black, T. A., Coursolle, C., Dunn, A. L., Barr, A. G., and Wofsy, S. C.: Comparison of carbon dioxide fluxes over three boreal black spruce forests in Canada, *Global Change Biol.*, 13, 89–107, 2007.

Bergh, J. and Linder, S.: Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands, *Global Change Biol.*, 5, 245–253, 1999.

**BGD**

5, 2707–2747, 2008

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- Bergh, J., McMurtrie, R. E., and Linder, S.: Climatic factors controlling the productivity of Norway spruce: a model-based analysis, *Forest Ecol. Manag.*, 110, 127–139, 1998.
- Bernacchi, C. J., Leakey, A. D. B., Heady, L. E., Morgan, P. B., Dohleman, F. G., McGrath, J. M., Gillespie, K. M., Wittig, V. E., Rogers, A., Long, S. P., and Ort, D. R.: Hourly and seasonal variation in photosynthesis and stomatal conductance of soybean grown at future CO<sub>2</sub> and ozone concentrations for 3 years under fully open-air field conditions, *Plant, Cell and Environ.*, 29, 2077–2090, 2006.
- Brooks, A. and Farquhar, G. D.: Effect of temperature on the CO<sub>2</sub>/O<sub>2</sub> specificity of ribulose 1,5-biphosphate carboxylase/oxygenase and the rate of respiration in the light, *Planta*, 165, 397–406, 1985.
- Dang, Q.-L., Margolis, H. A., and Collatz, G. J.: Parameterization and testing of a coupled photosynthesis-stomatal conductance model for boreal trees, *Tree Phys.*, 18, 141–153, 1998.
- De Pury, D. G. G. and Farquhar, G. D.: Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models, *Plant Cell Environ.*, 20, 539–557, 1997.
- Falge, E., Baldocchi, D., Tenhunen, J., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, Chr., Burba, G., Clement, R., Davis, K. J., Elbers, J. A., Goldstein, A. H., Grelle, A., Granier, A., Gudmundsson, J., Hollinger, D., Kowalski, A. S., Katul, G., Law, B. E., Malhi, Y., Meyers, T., Monson, R. K., Munger, J. W., Oechel, W., Paw U, K. T., Pilegaard, K., Rannik, Ü., Rebmann, C., Suyker, A., Valentini, R., Wilson, K., and Wofsy, S.: Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements, *Agr. Forest Meteorol.*, 113, 53–74, 2002.
- Farquhar, G. D., and von Caemmerer, S.: Modelling of photosynthetic response to environmental conditions, in: *Encyclopedia of Plant Physiology*, edited by: Lange, O. L., Nobel, P. S., Osmond, C. B., and Ziegler, H., 12B, 550–587, Berlin, Springer-Verlag, 1982.
- Farquhar, G. D., von Caemmerer S., and Berry, J. A.: A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C3 species, *Planta*, 149, 78–90, 1980.
- Grassi, G., Colom, M. R., and Minotta, G.: Effects of nutrient supply on photosynthetic acclimation and photoinhibition of one-year-old foliage of *Picea abies*, *Physiol. Plantarum*, 111, 245–254, 2001.
- Han, Q., Kawasaki, T., Nakano, T., and Chaba, Y.: Spatial and seasonal variability of temperature responses of biochemical photosynthesis parameters and leaf nitrogen content within a *Pinus densiflora* crown, *Tree Phys.*, 24, 737–744, 2004.

**BGD**

5, 2707–2747, 2008

---

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- Harley, P. C. and Baldocchi, D.: Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest, I. Leaf model parametrization, *Plant Cell Environ.*, 18, 1146–1156, 1995.
- Harrison, R. G., Jones, C. D., and Hughes, J. K.: Competing roles of rising CO<sub>2</sub> and climate change in the contemporary European carbon balance, *Biogeosciences*, 5, 1–10, 2008, <http://www.biogeosciences.net/5/1/2008/>.
- Hollinger, D. Y., Aber, J., Dail, B., Davidson, E. A., Goltz, S. M., Hughes, H., Leclerc, M. Y., Lee, J. T., Richardson, A. D., Rodriguez, C., Scotts, N. A., Achuatavari, D., and Walsh, J.: Spatial and temporal variability in forest atmosphere CO<sub>2</sub> exchange, *Global Change Biol.*, 10, 1689–1706, 2004.
- Janssens, I., Medlyn, B., Gielen, B., Laureysens, I., Jach, M. E., Van Hove, D., and Ceulemans, R.: Carbon budget of *Pinus sylvestris* saplings after four years of exposure to elevated atmospheric carbon dioxide concentration, *Tree Phys.*, 25, 325–337, 2005.
- Jurola, E., Aalto T., Thum, T., Vesala, T., and Hari, P.: Temperature dependence of leaf-level CO<sub>2</sub> fixation: revising biochemical coefficients through analysis of leaf three-dimensional structure, *New Phytol.*, 166, 205–216, 2005.
- Kattge, J. and Knorr, W.: Temperature acclimation in a biochemical model of photosynthesis: A reanalysis of data from 36 species, *Plant Cell Environ.*, 30, 1176–1190, 2007.
- Knorr, W. and Kattge, J.: Inversion of terrestrial ecosystem model parameter values against eddy covariance measurements by Monte Carlo sampling, *Global Change Biol.*, 11, 1333–1351, 2005.
- Kolari, P., Lappalainen, H. K., Hänninen, H.- and Hari, P.: Relationship between temperature and the seasonal course of photosynthesis in Scots pine at northern timberline and in southern boreal zone, *Tellus*, 59B, 542–552, 2007.
- Kosugi, Y., Shibata, S., and Kobashi, S.: Parameterization of the CO<sub>2</sub> and H<sub>2</sub>O gas exchange of several temperate deciduous broad-leaved trees at the leaf scale considering seasonal changes, *Plant Cell Environ.*, 26, 285–301, 2003.
- Kosugi, Y. and Matsuo, N.: Seasonal fluctuations and temperature dependence of leaf gas exchange parameters of co-occurring evergreen and deciduous trees in a temperate broad-leaved forest, *Tree Physiol.*, 26, 1173–1184, 2006.
- Kull, O. and Jarvis, P. G.: The role of nitrogen in a simple scheme to scale up photosynthesis from leaf to canopy, *Plant, Cell Environ.*, 18, 1174–1182, 1995.
- Law, B. E., Falge, E., Gu, L., Baldocchi, D., Bakwin, P., Berbigier, P., Davis, K., Dolman, A.

**BGD**

5, 2707–2747, 2008

---

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





---

**Seasonality of boreal  
coniferous forest CO<sub>2</sub>  
exchange**T. Thum et al.

---

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

J., Falk, M., Fuentes, J. D., Goldstein, A., Granier, A., Grelle, A., Hollinger, D., Janssens, I. A., Jarvis, P., Jensen, N. O., Katul, G., Mahli, Y., Matteucci, G., Meyers, T., Monson, R., Munger, W., Oechel, W., Olson, R., Pilegaard, K., Paw U. K. T., Thorgeirsson, H., Valentini, R., Verma, S., Vesala, T., Wilson, K., and Wofsy, S.: Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation, *Agr. Forest Meteorol.*, 113, 97–120, 2002.

Lawrie, J. and Hearne, J.: Reducing model complexity via output sensitivity, *Ecol. Model.*, 207, 137–144, 2007.

Leakey, A. D. B., Bernacchi, C. J., Ort, D. R., and Long, S. P.: Long-term growth of soybean at elevated [CO<sub>2</sub>] does not cause acclimation of stomatal conductance under fully open-air conditions, *Plant, Cell and Environ.*, 29, 1794–1800, 2006.

Leuning, R.: Scaling to a common temperature improves the correlation between photosynthesis parameters  $J_{max}$  and  $V_{c,max}$ , *J. Exp. Bot.*, 307, 345–347, 1997.

Leuning, R.: Temperature dependence of two parameters in a photosynthesis model, *Plant Cell Environ.*, 25, 1205–1210, 2002.

Lindroth, A., Lagergren, F., Aurela, M., Bjarnadottir, B., Christensen, T., Dellwik, E., Grelle, Ibrom, A., Johansson, T., Lankreijer, H., Launiainen, S., Laurila, T., Mölder, M., Nikinmaa, E., Pilegaard, K., Sigurdsson, B. D. and Vesala, T.: Leaf area index is the principal scaling parameter for both gross photosynthesis and ecosystem respiration of Northern deciduous and coniferous forests, *Tellus, B60*, 129–142, doi:10.1111/j.1600-0889.2007.00330.x, 2008.

Lloyd, J. and Taylor, J. A.: On the temperature dependence of soil respiration, *Funct. Ecol.*, 8, 315–323, 1994.

Lloyd, J., Wong, S. C., Styles, J.M., Batten, D., Priddle, R., Turnbull, C., and McConchie, C. A.: Measuring and modelling whole-tree gas exchange, *Aust. J. Plant Physiol.*, 22, 987–1000, 1995.

Luomala, E.-M., Laitinen, K., Kellomäki, S., and Vapaavuori, E.: Variable photosynthetic acclimation in consecutive cohorts of Scots pine needles during 3 years of growth at elevated CO<sub>2</sub> and elevated temperature, *Plant, Cell and Environ.*, 26, 645–660, 2003.

Luomala, E.-M., Laitinen, K., Sutinen, S., Kellomäki S., and Vapaavuori, E.: Stomatal density, anatomy and nutrient concentrations of Scots pine needles are affected by elevated CO<sub>2</sub> and temperature, *Plant, Cell and Environ.*, 28, 733–749, 2005.

Mäkelä, A., Pulkkinen, M., Kolari, P., Lagergren, F., Berbigier, P., Lindroth, A., Loustau, D., Nikinmaa, E., Vesala, T., and Hari, P.: Developing an empirical model of stand GPP with the

LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe, *Global Change Biol.*, 14, 92–108, 2008.

Markkanen, T., Rannik, Ü., Keronen, P., Suni, T., and Vesala, T.: Eddy covariance fluxes over a boreal Scots pine forest, *Boreal Environ. Res.*, 6, 65–78, 2001.

5 Medlyn, B. E., Dreyer, E., Ellsworth, D., Forstreuter, M., Harley, P. C., Kirschbaum, M. U. F., Le Roux, X., Montpied, P., Strassmeyer, J., Walcroft, A., Wang, K. and Loustau, D.: Temperature response of parameters of a biochemically based model of photosynthesis, II. A review of experimental data, *Plant, Cell and Environ.*, 25, 1167–1179, 2002a.

10 Medlyn, B. E., Loustau, D., and Delzon, S.: Temperature response of parameters of a biochemically based model of photosynthesis. I. Seasonal changes in mature maritime pine (*Pinus Pinaster* Ait.), *Plant, Cell and Environ.*, 25, 1155–1165, 2002b.

Medlyn, B. E., Berbigier, P., Clement, R., Grelle, A., Loustau, D., Linder, S., Wingate, L., Jarvis, P. G., Sigurdsson, B. D., and McMurtrie, R. E.: Carbon balance of coniferous forests growing in contrasting climates: Model-based analysis, *Agr. Forest Meteorol.*, 131, 97–124, 2005a.

15 Medlyn, B. E., Robinson, A. P., Clement, R., and McMurtrie, R. E.: On the validation of models of forest CO<sub>2</sub> exchange using eddy covariance data: some perils and pitfalls, *Global Change Biol.*, 25, 839–857, 2005b.

20 Moffat, A. M., Papale, D., Reichstein, M., Hollinger, D. Y., Richardson, A. D., Barr, A. G., Beckstein, C., Braswell, B. H., Churkina, G., Desai, A. R., Falge, E., Gove, J. H., Heimann, M., Hui, D., Jarvis, A. J., Kattge, J., Noormets, A., and Stauch, V. J.: Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes, *Agr. Forest Meteorol.*, 147, 209–232, 2007.

Pelkonen, P. and Hari, P.: The dependence of the springtime recovery of CO<sub>2</sub> uptake in Scots pine on temperature and internal factors, *Flora*, 169, 398–404, 1980.

25 Rannik, Ü., Kolari, P., Vesala, T., and Hari, P.: Uncertainties in measurement and modelling of net ecosystem exchange of a forest, *Agr. Forest Meteorol.*, 138, 244–257, 2006.

Rayment, M. B., Loustau, D., and Jarvis, P. G.: Photosynthesis and respiration of black spruce at three organizational scales: shoot, branch and canopy, *Tree Physiol.*, 22, 219–229, 2002.

30 Reichstein, M., Tenhunen, J., Rouspard, O., Ourcival, J.-M., Rambal, S., Miglietta, F., Peressotti, A., Pecchiari, M., Tirone, G., and Valentini, R.: Inverse modeling of seasonal drought effects on canopy CO<sub>2</sub>/H<sub>2</sub>O exchange in three Mediterranean ecosystems, *J. Geophys. Res.*, 108(D23), 4726, doi:10.1029/2003JD003430, 2003.

Repo, T., Hänninen, H., and Kellomäki, S.: The effects of long-term elevation of air temperature

**BGD**

5, 2707–2747, 2008

---

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- and CO<sub>2</sub> on the frost hardiness of Scots pine, *Plant Cell Environ.*, 19, 209–216, 1996.
- Repo, T., Leinonen, I., Wang, K.-Y., and Hänninen, H.: Relation between photosynthetic capacity and cold hardiness in Scots pine, *Physiol. Plantarum*, 126, 224–231, 2006.
- Ricciuto, D. M., Butler, M. P., Davis, K. J., Cook, B. D., Bakwin, P. S., Andrews, A., and Teclaw, R. M.: Causes of interannual variability in ecosystem-atmosphere CO<sub>2</sub> exchange in a northern Wisconsin forest using a Bayesian model calibration, *Agr. Forest Meteorol.*, 148, 309–327, 2008.
- Roberntz, P. and Stockfors, J.: Effects of elevated CO<sub>2</sub> concentration and nutrition on net photosynthesis, stomatal conductance and needle respiration of field-grown Norway spruce trees, *Tree Physiol.*, 18, 233–241, 1998.
- Sasai, T., Okamoto, K., Hiyama, T., and Yamaguchi, Y.: Comparing terrestrial carbon fluxes from the scale of a flux tower to the global scale, *Ecol. Model.*, 208, 135–144, 2007.
- Schulze, E.-D.: Biological control of the terrestrial carbon sink, *Biogeosciences*, 3, 147–166, 2006,  
<http://www.biogeosciences.net/3/147/2006/>.
- Sellers, P. J.: Canopy reflectance, photosynthesis and transpiration, *Int. J. Remote Sens.*, 6, 1335–1372, 1985.
- Sellers, P. J., Berry, J. A., Collatz, G. J., Field, C. B., and Hall, F. G.: Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme, *Remote Sens. Environ.*, 42, 187–216, 1992.
- Sellers, P. J., Los, S. O., Tucker, C. J., Justice, C. O., Dazlich, D. A. Collatz, G. J., and Randall, D. A.: A revised land surface parameterization (SiB2) for atmospheric GCMs. Part II: The generation of global fields of terrestrial biophysical parameters from satellite data, *J. Climate*, 9, 706–737, 1996.
- Solantie, R.: Daytime temperature sum – a new thermal variable describing growing season characteristics and explaining evapotranspiration, *Boreal Env. Res.*, 9, 319–333, 2004.
- Solantie, R.: Productivity of boreal forests in relation to climate and vegetation zones, *Boreal Env. Res.*, 10, 275–297, 2005.
- Steinbrecher, R., Hauff, K., Hakola, H., and Rössler, J.: A revised parameterization for emission modeling of isoprenoids for boreal plants. In: Biogenic VOC emissions and photochemistry in the boreal regions of Europe – Bihorep. Final report. Eds. T. Laurila and V. Lindfors. European Commission, 1999.
- Stenberg, P., De Lucia, E. H., Schoettle, A. W., and Smolander, H.: Photosynthetic light capture

**BGD**

5, 2707–2747, 2008

---

**Seasonality of boreal coniferous forest CO<sub>2</sub> exchange**T. Thum et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- and processing from cell to canopy, in: Resource physiology of conifers, edited by: Smith, W., Hinckley, T., and Roy, J., Academic Press, Ltd., London, 3–38, 1995.
- Stockfors, J. and Linder S.: The effect of nutrition on the seasonal course of needle respiration in Norway spruce stands, *Trees*, 12, 130–138, 1998.
- 5 Tanja, S., Berninger, F., Vesala, T., Markkanen, T., Hari, P., Mäkelä, A., Ilvesniemi, H., Hänninen, H., Nikinmaa, E., Huttula, T., Laurila, T., Aurela, M., Grelle, A., Lindroth, A., Arneeth, A., Shibistova, O., and Lloyd, J.: Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring, *Global Change Biol.*, 9, 1410–1426, 2003.
- Thornley, J. H. M.: Instantaneous canopy photosynthesis: Analytical expressions for sun and  
10 shade leaves based on exponential light decay down the canopy and an acclimated non-rectangular hyperbola for leaf photosynthesis, *Ann. Bot-London*, 89, 451–458, 2002.
- Thum, T., Aalto T., Laurila, T., Aurela, M., Kolari, P., and Hari, P: Parametrization of two photosynthesis models at the canopy scale in a northern boreal Scots pine forest, *Tellus*, 59B, 874–890, 2007.
- 15 Trenberth, K. E., Jones, P. D., Ambenje, P, Bojariu, R., Easterling, D., Klein Tank, A., Parker, D., Rahimzadeh, F., Renwick, J. A., Rusticucci, M., Soden, B., and Zhai, P: Observations: Surface and atmospheric climate change, in: *Climate Change 2007: The Physical Science Basis*, Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tiggner, M., and Miller, H. L., Cambridge University Press, United  
20 Kingdom and New York, NY, USA, 2007.
- Verbeeck, H., Samson, R., Verdonck, F. and Lemeur, R.: Parameter sensitivity and uncertainty of the forest carbon flux model FORUG: a Monte Carlo analysis, *Tree Phys.*, 26, 807–817, 2006.
- 25 Verbeeck, H., Samson, R., Granier, A., Montpied, P., and Lemeur, R.: Multi-year model analysis of GPP in a temperate beech forest in France, *Ecol. Model.*, 210, 85–103, 2008.
- Wang, K. Y., Kellomäki, S., and Laitinen, K.: Acclimation of photosynthetic parameters in Scots pine after three-year exposure to elevated CO<sub>2</sub> and temperature, *Agr. Forest Meteorol.*, 82, 195–217, 1996.
- 30 Wang, Y. P., Baldocchi, D., Leuning, R., Falge, E., and Vesala, T.: Estimating parameters in a land-surface model by applying nonlinear inversion to eddy covariance flux measurements from eight FLUXNET sites, *Global Change Biol.*, 12, 1–19, 2006.
- Wang, Q., Tenhunen, J., Falge, E., Bernhofer C. H., Granier, A. and Vesala, T.: Simulation

---

**Seasonality of boreal  
coniferous forest CO<sub>2</sub>  
exchange**T. Thum et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



and scaling of temporal variation in gross primary production for coniferous and deciduous temperate forest, *Global Change Biol.*, 10, 37–51, 2003.

Way, D. A. and Sage, R. F.: Elevated growth temperatures reduce the carbon gain of black spruce [*Picea mariana* (Mill.) B.S.P.], *Global Change Biol.*, 14, 623–636, 2008.

5 Wilson, K. B., Baldocchi, D., and Hanson, P. J.: Leaf age affects the seasonal pattern of photosynthetic capacity and net ecosystem exchange of carbon in a deciduous forest, *Plant Cell Environ.*, 24, 571–583, 2001.

Wu, Y., Brashers, B., Finkelstein, P. L., and Pleim, J. E.: A multilayer biochemical dry deposition model, 1. Model formulation. *J. Geophys. Res.*, 108, 4013–4025, 2003.

10 Wullschleger, S. D.: Biochemical limitations to carbon assimilation in C3 plants – A retrospective analysis of the  $A/C_i$  curve from 109 species, *J. Exp. Bot.*, 44, 907–920, 1993.

Xu, L. and Baldocchi, D.: Seasonal trends in photosynthetic parameters and stomatal conductance of blue oak (*Quercus douglasii*) under prolonged summer drought and high temperature, *Tree Phys.*, 23, 865–877, 2003.

15

**BGD**

5, 2707–2747, 2008

---

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Seasonality of boreal  
coniferous forest CO<sub>2</sub>  
exchange

T. Thum et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Table 1.** The fitting parameters  $f$  and  $E$  for  $J_{\max}$  and  $V_{c(\max)}$  from Eq. (3) for all the time periods in the parameterization year. Also the value of the biochemical model parameter at 17 °C shown for each fit.

Site	$f$	$E$	value at 17 °C
Parameter $J_{\max}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )			
Sodankylä			
Spring (1 May–3 June)	101.5	82 928	40.3
Summer (4 June–30 September)	142.1	75 031	61.7
Kenttäröva			
Spring (May)	71.0	72 676	31.6
Summer (June–August)	101.4	61 309	51.3
Norunda			
Spring and summer (April–October)	144.0	88 057	54.1
Hyytiälä			
Spring (April)	6.2	9 852	5.6
Summer (May–August)	100.5	64 890	48.8
Autumn (September)	43.1	34 256	29.5
Parameter $V_{c(\max)}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )			
Sodankylä			
Spring (1 May–3 June)	13.9	75 477	6.0
June (4 June–24 June)	23.6	86 446	9.9
Summer (25 June–August)	40.3	84 152	15.8
Kenttäröva			
Spring (May)	13.0	68 024	6.1
Summer (June–August)	21.5	64 911	10.5
Norunda			
Spring (1 March–19 April)	2.6	31 626	1.9
Summer (20 April–30 September)	25.4	73 591	11.2
Hyytiälä			
Spring (April)	1.5	310.0	1.6
Spring II (May)	4.6	14 381	3.9
Summer II (June–August)	25.0	78 648	10.4
Autumn (September)	15.2	50 147	8.7

Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.

**Table 2.** The  $r^2$  values (model vs. measurement) for the whole growing season ( $r_{GS}^2$ ) and summertime with each sites' own parameterization ( $r_{ST}^2$ ) and  $r^2$  for each site using the summertime parameterization of Hyttiälä ( $r_{ST,HYY}^2$ ). P in parenthesis after the year denotes the year used for parameterization.

Site	Year	$r_{GS}^2$	$r_{ST}^2$	$r_{ST,HYY}^2$
Norunda	1999	0.63	0.62	0.62
	2001 (P)	0.59	0.58	0.57
	2002	0.58	0.57	0.55
Hyttiälä	2000	0.75	0.76	0.76
	2001 (P)	0.81	0.78	0.78
Kenttäröva	2003	0.62	0.58	0.57
	2004	0.63	0.61	0.60
	2005	0.61	0.59	0.56
	2006 (P)	0.62	0.61	0.60
Sodankylä	2001 (P)	0.70	0.75	0.69
	2002	0.61	0.65	0.60
	2003	0.60	0.64	0.53
	2004	0.67	0.71	0.65
	2005	0.59	0.70	0.63

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Seasonality of boreal  
coniferous forest CO<sub>2</sub>  
exchange

T. Thum et al.

**Table 3.** Literature values for the biochemical model parameters.

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

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

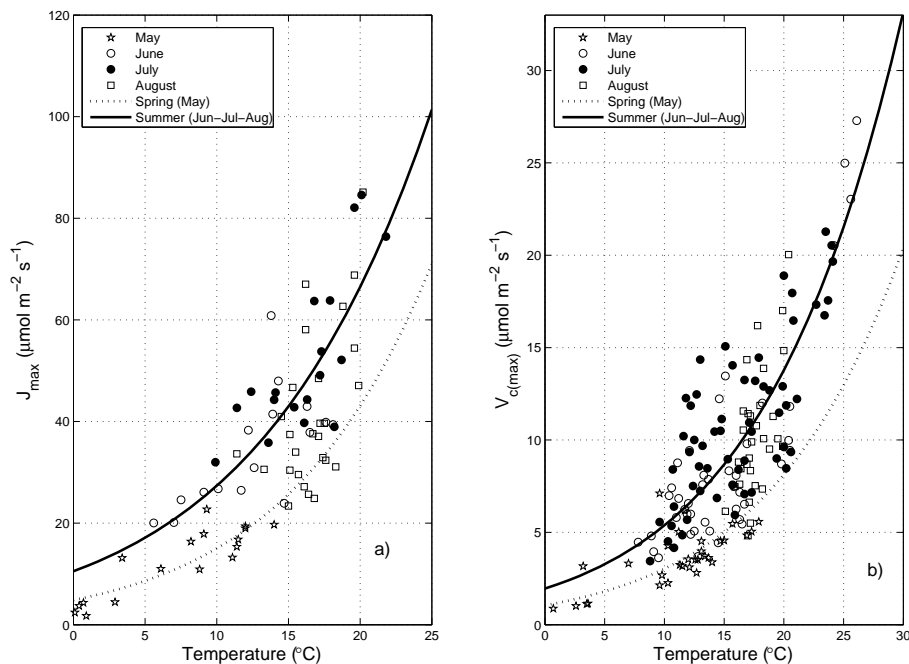
Interactive Discussion





Seasonality of boreal  
coniferous forest CO<sub>2</sub>  
exchange

T. Thum et al.

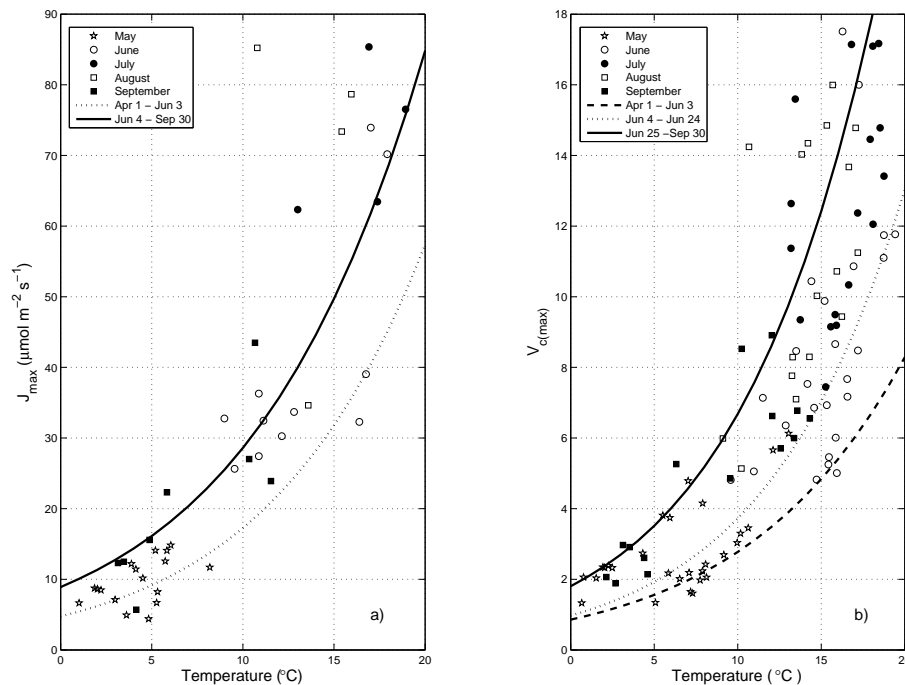


**Fig. 1.** The temperature responses of the biochemical model parameters  $J_{\max}$  (a) and  $V_{c(\max)}$  (b) for spruce forest at Kenttäröva in 2006. The springtime (1–31 May) temperature fit is shown as a dashed line. The points were obtained by model inversion from half-hourly eddy covariance data.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Seasonality of boreal  
coniferous forest CO<sub>2</sub>  
exchange

T. Thum et al.



**Fig. 2.** The temperature responses of the biochemical model parameters  $J_{\max}$  (a) and  $V_{c(\max)}$  (b) for homogeneous Scots pine forest at Sodankylä in 2001. The time periods of the temperature fits are shown in the legend.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

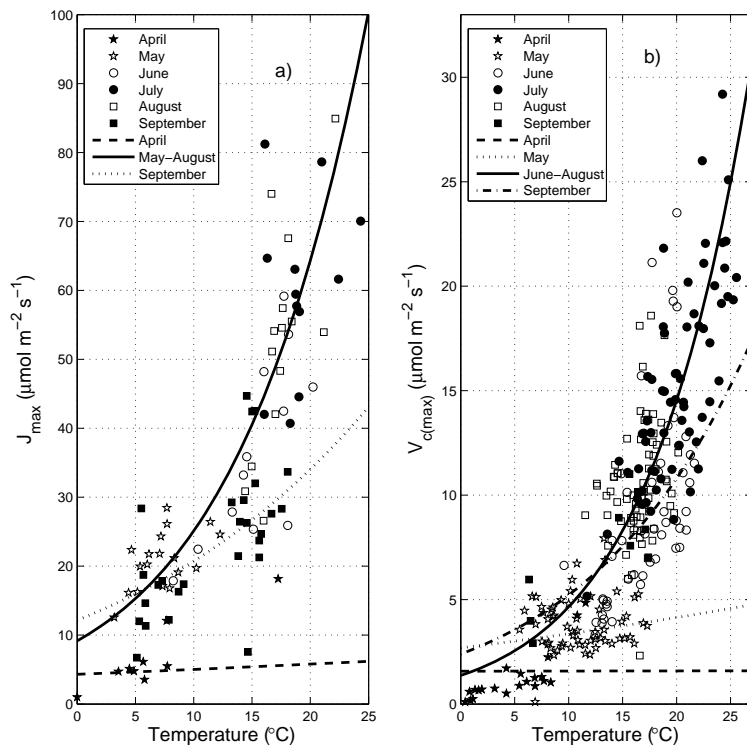
Full Screen / Esc

Printer-friendly Version

Interactive Discussion

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.



**Fig. 3.** The temperature responses of the biochemical model parameters  $J_{\max}$  (a) and  $V_{c(\max)}$  (b) for Scots pine dominated forest at Hyytiälä in 2001.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

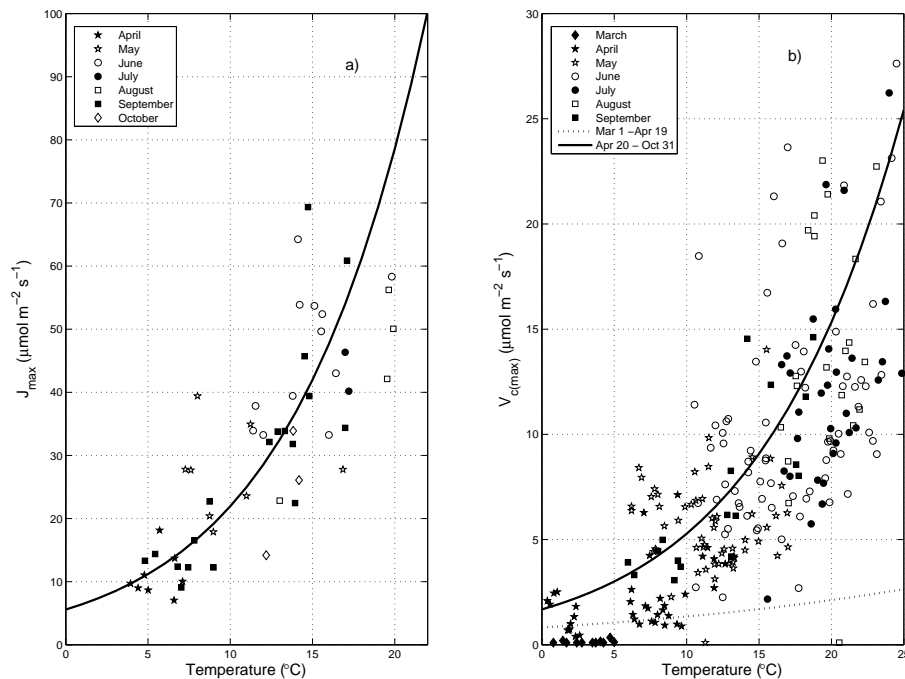
Printer-friendly Version

Interactive Discussion



## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.



**Fig. 4.** The temperature responses of the biochemical model parameters  $J_{\max}$  (a) and  $V_{c(\max)}$  (b) for coniferous forest at Norunda in 2001. There is only one temperature response curve fitted for the parameter  $J_{\max}$ .

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

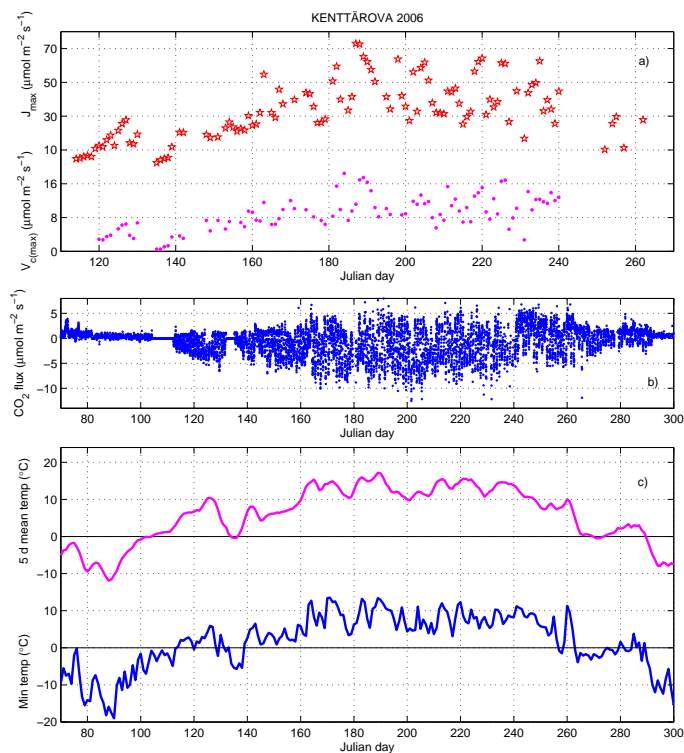
Printer-friendly Version

Interactive Discussion



Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.



**Fig. 5.** Various parameters for Kenttäröva in 2006 as a function of day-of-the-year. **(a)** 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).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

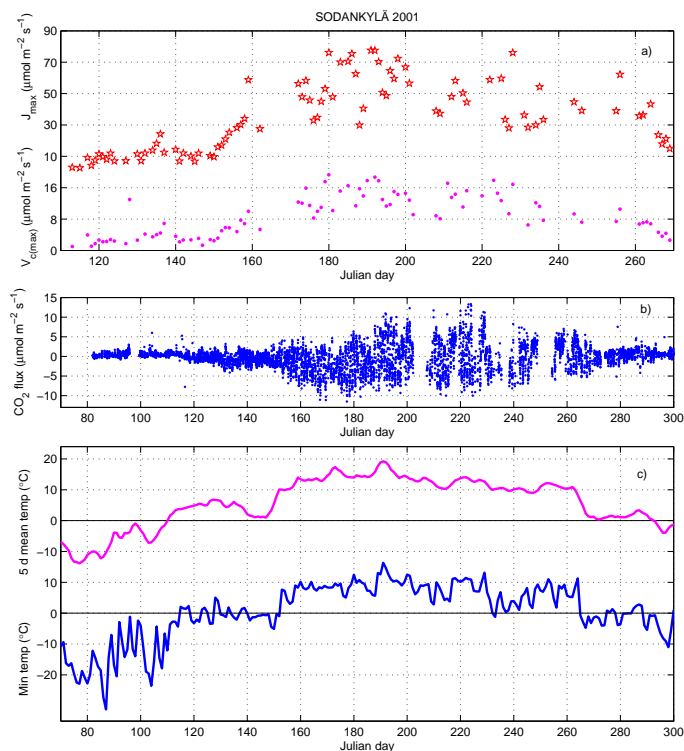
Printer-friendly Version

Interactive Discussion



Seasonality of boreal  
coniferous forest CO<sub>2</sub>  
exchange

T. Thum et al.

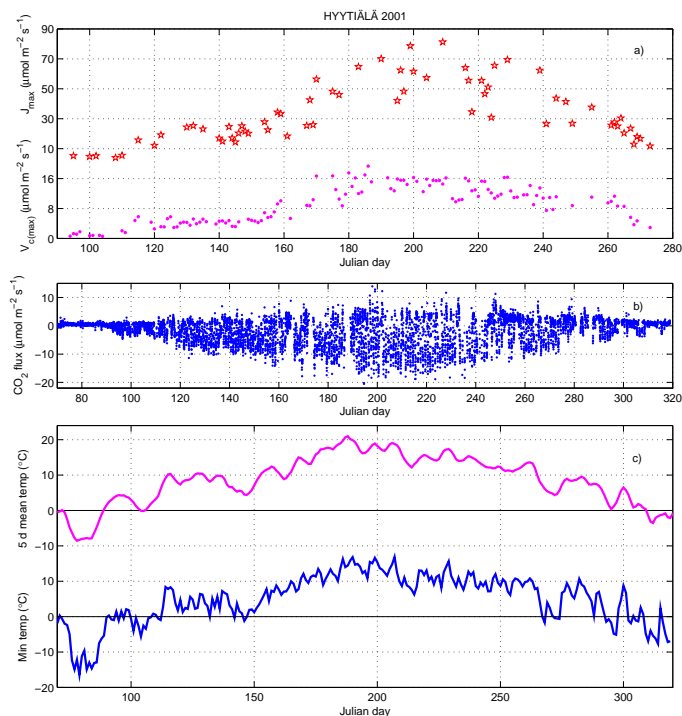


**Fig. 6.** Various parameters for Sodankylä in 2001 as a function of day-of-the-year. **(a)** Inverted daily values of the biochemical parameters  $J_{\text{max}}$  (red symbols) and  $V_{C(\text{max})}$  (magenta symbols); **(b)** eddy covariance flux measurements; **(c)** five-day average air temperature (magenta line) and minimum air temperature (blue line).

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Seasonality of boreal  
coniferous forest CO<sub>2</sub>  
exchange

T. Thum et al.

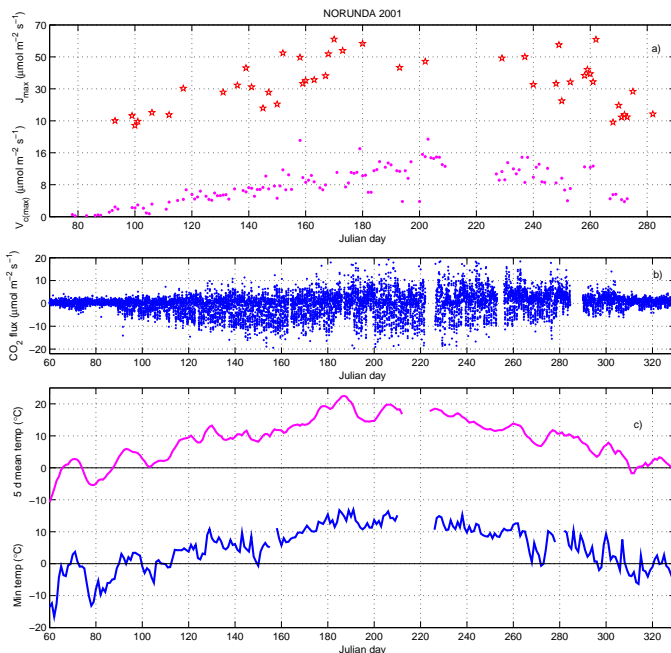


**Fig. 7.** Various parameters for Hyytiälä in 2001 as a function of day-of-the-year. **(a)** Inverted daily values of the biochemical parameters  $J_{\max}$  (red symbols) and  $V_{c(\max)}$  (magenta symbols); **(b)** eddy covariance flux measurements; **(c)** five-day average air temperature (magenta line) and minimum air temperature (blue line).

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.



**Fig. 8.** Various parameters for Norunda in 2001 as a function of day-of-the-year. **(a)** 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).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

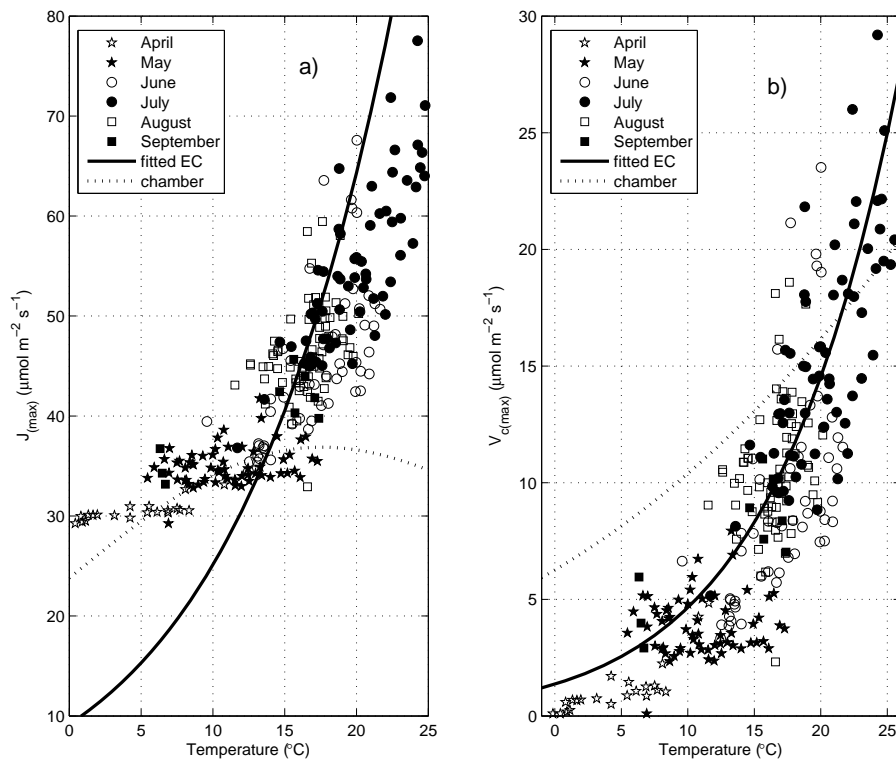
Interactive Discussion





## Seasonality of boreal coniferous forest CO<sub>2</sub> exchange

T. Thum et al.



**Fig. 9.** The symbols in (a) denote the  $J_{\max}$  values obtained by inversion using the relationship represented in Eq. (4) between  $J_{\max}$  and  $V_{c(\max)}$  at Hyttälä. In (b) the symbols denote the  $V_{c(\max)}$  values obtained by inversion at Hyttälä. The solid line shows the fit from the previous inversion during the summer period (same as symbols in (b)), while the dashed lines show the temperature dependencies obtained from chamber measurements (Aalto et al., 2002). The fits from chamber measurements are shown over a larger temperature range than to which they were fitted.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

