

FINNISH METEOROLOGICAL INSTITUTE  
CONTRIBUTIONS  
No. 81

MODELLING BOREAL FOREST CO<sub>2</sub> EXCHANGE AND SEASONALITY

Tea Thum

Division of Atmospheric Sciences and Geophysics  
Department of Physics  
Faculty of Science  
University of Helsinki  
Helsinki, Finland

Academic dissertation

To be presented, with the permission of the Faculty of Science of the University of Helsinki,  
for public criticism in auditorium D101, Gustaf Hällströmin katu 2, in Helsinki on 4  
December 2009, at 12 noon.

Finnish Meteorological Institute  
Helsinki, 2009

ISBN 978-951-697-707-5 (paperback)  
ISSN 0782-6117  
Yliopistopaino  
Helsinki 2009

ISBN 978-951-697-708-2 (E-thesis version)  
<http://ethesis.helsinki.fi/>  
Helsinki 2009  
Helsingin yliopiston verkkojulkaisut



FINNISH METEOROLOGICAL INSTITUTE

Published by Finnish Meteorological Institute  
(Erik Palménin aukio 1), P.O. Box 503  
FIN-00101 Helsinki, Finland

Series title, number and report code of publication  
Contributions No. 81, FMI-CONT-81

Date: December 2009

Authors Name of project  
Tea Thum

Title  
Modelling boreal forest CO<sub>2</sub> exchange and seasonality

Abstract

Man-induced climate change has raised the need to predict the future climate and its feedback to vegetation. These are studied with global climate models; to ensure the reliability of these predictions, it is important to have a biosphere description that is based upon the latest scientific knowledge. This work concentrates on the modelling of the CO<sub>2</sub> exchange of the boreal coniferous forest, studying also the factors controlling its growing season and how these can be used in modelling. In addition, the modelling of CO<sub>2</sub> gas exchange at several scales was studied.

A canopy-level CO<sub>2</sub> gas exchange model was developed based on the biochemical photosynthesis model. This model was first parameterized using CO<sub>2</sub> exchange data obtained by eddy covariance (EC) measurements from a Scots pine forest at Sodankylä. The results were compared with a semi-empirical model that was also parameterized using EC measurements. Both of the models gave satisfactory results. The biochemical canopy-level model was further parameterized at three other coniferous forest sites located in Finland and Sweden. At all the sites, the two most important biochemical model parameters showed seasonal behaviour, i.e., their temperature responses changed according to the season. Modelling results were improved when these changeover dates were related to temperature indices. During summer-time the values of the biochemical model parameters were similar at all the four sites.

Different control factors for CO<sub>2</sub> gas exchange were studied at the four coniferous forests, including how well these factors can be used to predict the initiation and cessation of the CO<sub>2</sub> uptake. Temperature indices, atmospheric CO<sub>2</sub> concentration, surface albedo and chlorophyll fluorescence (CF) were all found to be useful and have predictive power. In Finnish Lapland a trend toward an earlier start of the CO<sub>2</sub> uptake in spring was also observed. In addition, a detailed simulation study of leaf stomata in order to separate physical and biochemical processes was performed, and the possibility of detecting CF by passive devices in coniferous forests was assessed. The simulation study brought to light the relative contribution and importance of the physical transport processes, while the passive detection of CF was found to be feasible.

The results of this work can be used in improving CO<sub>2</sub> gas exchange models in boreal coniferous forests. The meteorological and biological variables that represent the seasonal cycle were studied, and a method for incorporating this cycle into a biochemical canopy-level model was introduced.

Publishing unit		
Finnish Meteorological Institute, Climate Change Research		
Classification (UDK)	Keywords	
504.064	biochemical model, leaf stomata model, eddy covariance,	
551.586	chlorophyll fluorescence	
ISSN and series title	Finnish Meteorological Institute Contributions	
0782-6117		
ISBN	Language	
978-951-697-707-5	English	
Sold by	Pages 140	Price
Finnish Meteorological Institute / Library		
P.O.Box 503, FIN-00101 Helsinki, Finland	Note	

Julkaisija Ilmatieteen laitos,  
( Erik Palménin aukio 1 )  
PL 503, 00101 Helsinki

Julkaisuaika: Joulukuu 2009

Tekijä(t) Projektiin nimi  
Tea ThumNimeke  
Boreaalisen metsän CO<sub>2</sub>-vaihdon sekä vuodenaikaisuusvaihtelun mallittaminen  
Tiivistelmä

Ilmastonmuutos on aiheuttanut tarpeen ennustaa tulevaisuuden ilmastoa sekä ilmaston takaisinkytkentää kasvillisuuden kanssa. Näitä asioita tutkitaan ilmastomalleilla. Jotta mallien antamat ennusteet olisivat mahdollisimman luotettavia, on tärkeää, että mallien biösfäärikuvaus on tämänhetkisen tieteellisen tietämyksen tasolla. Tämä työ keskittyy hiilidioksidinvaihdon mallittamiseen boreaalisisessa metsässä, kasvukautta rajoittavien tekijöiden tutkimiseen sekä niiden mallitussovelluksiin. Lisäksi hiilidioksidinvaihtoa tutkittiin useilla eri skaaloilla.

Lehvästötason hiilidioksidi (CO<sub>2</sub>)-kaasunvaihtomalli kehitettiin biokemialliseen fotosynteesimallin pohjalta. Malli parametrisoitiin käyttäen mikrometeorologisia CO<sub>2</sub>-kaasunvaihtomittauksia Sodankylän mäntymetsästä. Myös semiempiirinen fotosynteesimalli parametrisoitiin käyttäen samoja mittauksia, jonka jälkeen kahden mallin antamia tuloksia verrattiin mittauksiin. Molemmat mallit antoivat tyydyttäviä tuloksia. Biokemiallinen lehvästötason malli parametrisoitiin edelleen kolmelle muulle havumetsälle, jotka sijaitsivat Suomessa ja Ruotsissa. Kaikilla näillä metsäpaikoilla kahdessa tärkeimmässä biokemiallisen mallin parametrissa näkyi vuodenaikaisuusvaihtelu, täten niiden lämpötilavaste vaihtui vuodenajan mukaisesti. Mallitustulokset paranivat kun näiden vasteiden vaihtumispäivät sidottiin lämpötilaindekseihin. Kesäaikana biokemiallisen mallin parametrit olivat samanlaisia kaikilla neljällä metsäpaikalla.

Erilaisia CO<sub>2</sub>-kaasunvaihdon määrääviä tekijöitä tutkittiin näillä neljällä eri havumetsäpaikalla, keskittyen erityisesti siihen kuinka näitä tekijöitä voidaan käyttää vuotuisen CO<sub>2</sub>-kaasunvaihdon alun sekä hiipumisen ennustamiseen. Lämpötilaindeksit, ilmakehän CO<sub>2</sub>-pitoisuus, pinta-albedo ja klorofyllifluoresenssi olivat kaikki hyödyllisiä ja ennustuskakyisiä muuttujia. Suomen Lapissa havaittiin trendi CO<sub>2</sub>-vaihdon aikaisempaan alkamisajankohtaan keväällä. Lisäksi tehtiin yksityiskohtainen simulaatio lehden ilmarasta fysikaalisten ja biokemiallisten prosessien erottamiseksi, sekä tutkittiin mahdollisuutta havaita klorofyllifluoresenssia havumetsässä passiivisilla mittausten menetelmillä. Ilmarakosimulaatio valotti fysikaalisten siirtoilmioiden suhteellista osuutta ja tärkeyttä, ja klorofyllifluoresenssin passiivinen havainnointi osoittautui mahdolliseksi.

Tämän työn tuloksia voidaan käyttää boreaalisten metsien CO<sub>2</sub>-kaasunvaihtoa kuvaavien mallien parantamiseen. Työssä tutkittiin vuodenaikaisuuskykyä kuvaavia meteorologisia ja biologisia muuttujia sekä esiteltiin menetelmä, joilla nämä muuttajat saadaan yhdistettyä biokemialliseen lehvästötason malliin.

Julkaisijayksikkö  
Ilmatieteen laitos, IlmastonmuutostutkimusLuokitus (UDK) Asiasanat  
504.064 biokemiallinen malli, ilmarakomalli, kovarianssimenetelmä,  
551.586 klorofyllifluoresenssiISSN ja avainnime  
0782-6117ISBN Kieli  
978-951-697-707-5 Englanti

Myynti Sivumäärä 140 Hinta

Ilmatieteen laitos / Kirjasto Lisätietoja  
PL 503, 00101 Helsinki

## **Acknowledgements**

This work has been done at the Finnish Meteorological Institute. I thank Yrjö Viisanen and Ari Laaksonen for providing excellent working facilities and good working atmosphere.

Thanks are due to the whole Greenhouse Gases group, especially to Tuomas Laurila, the head of the group, and Docent Tuula Aalto, the primary supervisor of this work. Tuomas Laurila provided me with the opportunity to work in his group, while Tuula Aalto guided me throughout this work.

I also wish to thank my other supervisors Professor Timo Vesala and Docent Jari Liski for their contribution to this work.

In addition, numerous other people have contributed to this work. I express my gratitude to my co-authors Dr. Mika Aurela, Juha Hatakka, Dr. Eija Juurola, Pasi Kolari, Professor Pertti Hari and Professor Anders Lindroth, as well as to the whole team contributing to the SIFLEX-project in 2002. Warmest thanks also to Dr. Sanna Sevanto for encouragement and cooperation.

I thank the pre-examiners, Professor Annikki Mäkelä and Dr. Tiina Markkanen, for their excellent and constructive comments on this work. For grammatical corrections to the articles as well as to the summary part of this thesis, I thank Robin King.

The Maj and Tor Nessling Foundation (project 'Soil carbon in Earth System Models'; coordinators Docent Jari Liski and Professor Heikki Järvinen), the Academy of Finland (Finnish Center of Excellence 'Research Unit on Physics, Chemistry and Biology of Atmospheric Composition and Climate Change'; coordinator Professor Markku Kulmala) and the Nordic Council of Ministers (project 'Nordic Centre for Studies of Ecosystem Carbon Exchange and its Interactions with the Climate System'; coordinator Professor Anders Lindroth) are acknowledged for their financial support.

Finally, I would like to thank my family and friends for their continuous support throughout this work. Especially I want to thank Ahmed for his encouragement and caring.

Helsinki, December 2009

Tea Thum

# Contents

<b>List of original publications.....</b>	<b>7</b>
<b>Author's contribution.....</b>	<b>8</b>
<b>1 Introduction.....</b>	<b>9</b>
<b>2 Outline and aims of this work.....</b>	<b>11</b>
<b>3 Theory, measurements and models.....</b>	<b>12</b>
3.1. Theory.....	12
3.1.1. Leaf-level CO <sub>2</sub> exchange.....	12
3.1.2. Canopy-level CO <sub>2</sub> exchange.....	16
3.1.3. Seasonality of the boreal forest.....	18
3.2. Model description.....	22
3.2.1. The biochemical model.....	22
3.2.2. Optimal stomatal control model.....	24
3.2.3. Upscaling the leaf-level model.....	25
3.2.4. Three-dimensional (3-D) leaf model.....	26
3.3. Measurements.....	26
3.3.1. Measurement sites.....	26
3.3.2. Leaf chamber CO <sub>2</sub> exchange measurements.....	27
3.3.3. Eddy covariance measurements.....	28
3.3.4. Chlorophyll fluorescence measurements.....	29
3.3.5. CO <sub>2</sub> concentration measurements.....	29
<b>4 Results.....</b>	<b>30</b>
4.1. Redefining the biochemical model parameters at leaf-level.....	30
4.2. Comparison of results from two upscaled leaf-level models.....	32
4.3. Assessing seasonality through parameters in a canopy-level model.....	35
4.4. Tracking seasonality with meteorological and biological variables.....	36
<b>5 Discussion.....</b>	<b>38</b>
<b>6 Conclusions.....</b>	<b>42</b>
<b>References.....</b>	<b>43</b>

## List of original publications

### Paper I

Juurola, E., Aalto, T., Thum, T., Vesala, T., and Hari, P., 2005. Temperature dependence of leaf-level CO<sub>2</sub> fixation: revising biochemical coefficients through analysis of leaf three-dimensional structure. *New Phytologist* 166, 205-215.

### Paper II

Thum, T., Aalto, T., Laurila, T., Aurela, M., Kolari, P., and Hari, P., 2007. Parametrization of two photosynthesis models at the canopy scale in a northern boreal Scots pine forest. *Tellus* 59B, 874-890.

### Paper III

Thum, T., Aalto, T., Laurila, T., Aurela, M., Lindroth, A., and Vesala, T., 2008. Assessing seasonality of biochemical CO<sub>2</sub> exchange model parameters from micrometeorological flux observations at boreal coniferous forest. *Biogeosciences* 5, 1625-1639.

### Paper IV

Thum, T., Aalto, T., Laurila, T., Aurela, M., Hatakka, J., Lindroth, A., and Vesala, T., 2009. Spring initiation and autumn cessation of boreal coniferous forest CO<sub>2</sub> exchange assessed by meteorological and biological variables. *Tellus* 61B, 701-717.

### Paper V

Lous, J., Ounis, A., Ducruet, J.-M., Evain, S., Laurila, T., Thum, T., Aurela, M., Wingsle, G., Alonso, L., Pedros, R., and Moya, I., 2005. Remote sensing of sunlight-induced chlorophyll fluorescence and reflectance of Scots pine in the boreal forest during spring recovery. *Remote Sensing of Environment* 96, 37-48.

## **Author's contribution**

**Paper I:** The author of this thesis did part of the simulations, and was involved in interpretation of the results and the writing of the paper.

**Papers II, III, IV:** The author did the model development, all the figures and data analysis (except the CO<sub>2</sub> concentration data analysis in **Paper IV**) and bore the main responsibility for writing the papers.

**Paper V:** The author was involved in the measurements, the interpretation of the results and the writing of the paper.

**Paper I** has also been used in the Ph.D. thesis of E. Juurola (major: forest ecology).



# 1. Introduction

Human activities have increased the concentration of atmospheric carbon dioxide (CO<sub>2</sub>), thus causing climatic change leading to increasing air temperatures and changing precipitation patterns (IPCC, 2007). To predict these changes and facilitate their mitigation, global climate models have been developed. These models predict forthcoming climate using different anthropogenic emission scenarios. The global climate models react to these conditions according to the processes that have been modelled in them. The quality of the models, that is, how realistically the different processes have been modelled, has an impact on the predictions that are used as the basis for mitigation plans. It is therefore important to keep the models up-to-date with our current scientific knowledge.

The global carbon cycle is composed of carbon exchange between the atmosphere, ocean and terrestrial ecosystems. In the terrestrial carbon cycle, the vegetation takes up carbon and stores it into biomass and soils, while carbon is released back into the atmosphere through respiration by plants and the decomposition of soil carbon by microbes.

Terrestrial vegetation has an impact on climate and the global carbon cycle (Foley et al., 2003). The global CO<sub>2</sub> concentration has increased from a pre-industrial level of 270 ppm to its current value of 379 ppm (2005), the growth rate (between the years 1995-2005) being 1.9 ppm yr<sup>-1</sup> (IPCC, 2007). Not all the anthropogenic CO<sub>2</sub> emissions remain in the atmosphere: approximately half of these emissions have been taken up by the terrestrial vegetation and oceans (Ciais et al., 2000). Currently there are some indications that the terrestrial sink is diminishing (Canadell et al., 2007), thus leaving more anthropogenic CO<sub>2</sub> in the atmosphere and accelerating the climate change. A better understanding of the global and terrestrial carbon cycle would yield us better predictions of future changes.

Boreal forest, or taiga, mostly consisting of coniferous trees, is one of the world's largest biomes and an essential part of the terrestrial carbon cycle (Gurevitch et al., 2002). The boreal forests influence the earth's climate (Bonan et al., 1995; Foley et al., 2003; Bonan, 2008b). In a study in which the influences of all the major biomes of the world on global temperature were assessed, the boreal forests were assessed as having the greatest biogeophysical effect on annual global temperature (Snyder et al., 2004). The boreal forests constitute a significant carbon storage (Gover et al., 2001) and a large carbon sink (Goodale et al., 2002; Dong et al., 2003).

A drastic increase in temperature, between 2.3 and 7.4 °C by the end of this century, has been projected by climate models to occur at high latitudes, where the boreal forests are located (IPCC, 2007). Warming will cause changes in the ecosystem functioning: with a temperature increase of 3 °C even a dieback of boreal forests has been predicted (Lenton et al., 2008). Even without this extreme scenario, changes are likely to occur. The influence of these changes on the carbon balance of the boreal forests has been studied, focusing on whether they will become a carbon source or a stronger carbon sink (Piao et al., 2007).

Recently a number of studies have found changes in the greenness and photosynthetic activity in high latitudes, indicating a longer growing season (Myneni et al., 1997; Slayback et al., 2003; Karlsen et al., 2007; Bronson et al., 2009), but it is not clear if this will increase the carbon sink of the boreal forests. In some studies the lengthening of the growing season has increased the carbon sink (Churkina et al., 2005), while in others the opposite has been found (Dunn et al., 2007). An earlier onset of photosynthesis in the spring will lengthen the time for which the forest takes up carbon, enhancing the carbon sink (Ensminger et al., 2004). On the other hand, warmer autumns are likely to increase the release of carbon. The diminishing of photosynthesis occurs concurrently with decreasing light, but if the temperatures remain high in the autumn, respiration will continue (Piao et al., 2008; Vesala et al., 2009).

The CO<sub>2</sub> exchange of the forest ecosystems has been studied on many scales by measurements and modelling. In addition to traditional leaf chambers, a widespread network of eddy covariance (EC) measurement sites has been established during the last two decades (Baldocchi, 2003). The EC method enables continuous measurements of the whole ecosystem gas exchange routinely for the first time. These data can be used to further develop CO<sub>2</sub> gas exchange models, including those used in the global climate models. Global climate models model the whole globe, regional models simulate smaller systems, plot-scale models deal with the ecosystem level, and these models downscale to the plant or leaf scale; from this scale, one can further focus on the stomata and molecular scales. These biological multiscale systems can be modelled using a methodological framework of systems theory and hierarchy theory (Mäkelä, 2003). A biological multiscale system can be considered to be a hierarchical system that consists of several organizational levels, e.g., cells, tissues, organs, plant, forest (Thornley and Johnson, 1990). Each of these levels has its own unique language, and is an integration of items from a lower level. For a given level to operate successfully, the lower levels are also required to function properly. Lower levels obtain their boundary conditions and driving functions from the upper levels. Higher levels generally have slower processes, whereas lower levels are characterized by faster process rates as well as smaller physical size (Thornley and Johnson, 1990; Mäkelä, 2003). The multiscale character of the global carbon cycle model brings up the issue of whether all the significant processes at lower levels are included in the higher levels, and whether all the levels are parameterized appropriately in the light of the measurements.

Lately, remote sensing data has been used to observe the seasonal development of the vegetation at a regional level (Myneni et al., 1997), and these measurements have also been incorporated into terrestrial ecosystem models (Knorr and Heimann, 2001b). The remote sensing of chlorophyll fluorescence has advanced (Meroni et al., 2009). The start of the snow melt, as assessed by remote sensing, has been connected to the beginning of the CO<sub>2</sub> exchange of the vegetation (Bartsch et al., 2007). These developments open new vistas for modelling of CO<sub>2</sub> gas exchange.

## 2. Outline and aims of this work

This work concentrates on the modelling of CO<sub>2</sub> gas exchange at different scales, from a leaf stomata to forest canopies, and the inclusion of the seasonal cycle into the modelling. At the stomatal scale the mesophyll conductance is a significant factor, and it may play a role even at larger scales. Mesophyll cells are the cells inside the leaf in which the photosynthesis occurs. Often mesophyll conductance is neglected in leaf and canopy level models, since not enough information about it is available for it to be incorporated or parameterized in the models. Mesophyll conductance is dependent on the physical and environmental conditions inside the leaf. New computing resources have made more detailed gas exchange simulations possible, and thus the effect of mesophyll conductance can also be assessed.

Wang (1996) used leaf-level measurements of CO<sub>2</sub> gas exchange to derive an empirical seasonal cycle of biochemical model parameters. This kind of seasonal cycle is neglected in present-day models, even though it has been shown that the modelling of terrestrial carbon cycle - climate feedback is sensitive to the description of photosynthetic capacity and its temperature response that is adopted (Matthews et al., 2007), and the seasonality of the vegetation still needs improvements (Sasai et al., 2007). We used EC data, year-round gas exchange observations, and auxiliary meteorological and biological measurements to assess how the seasonal cycle can best be followed and how it can be implemented in the modelling.

In addition, canopy-level CO<sub>2</sub> gas exchange models have often been parameterized using leaf-level measurements. This might lead to some biases in canopy-level modelling, since scaling from a leaf to a canopy raises complex questions, and it might be better to use ecosystem-scale measurements to estimate model parameters at ecosystem and larger scales (Wang et al., 2006). The EC data available today allow parameterization of model parameters at the canopy scale.

To summarize, the aims of this thesis were

- to evaluate the role of physical vs. biochemical processes at the leaf stomata scale
- to find the best environmental or biological variable to describe the seasonal status of a boreal forest and through this the implementation of seasonality into CO<sub>2</sub> gas exchange modelling
- to determine the parameters for canopy-level CO<sub>2</sub> gas exchange models using eddy covariance data

In Chapter 3.1 the theoretical background for photosynthesis, forest CO<sub>2</sub> fluxes and the seasonality of the boreal forests is first presented. Chapter 3.2 introduces the biochemical model and the optimal stomatal control model, and discusses how they were upscaled to the canopy level. The 3-D leaf stomata model is also described. The measurements are

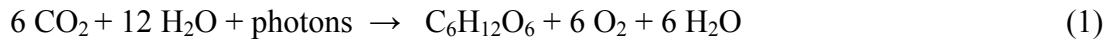
described in Chapter 3.3. These include EC measurements at four coniferous sites as well as leaf chamber, chlorophyll fluorescence and CO<sub>2</sub> concentration measurements. Chapter 4 presents the main results of this work. The three-dimensional leaf stomata model was used to study the temperature dependencies of the different processes taking part in the CO<sub>2</sub> gas exchange, while two different photosynthesis models were upscaled to the canopy level and their results were compared. In addition, the seasonal cycle of the model parameters and environmental variables were studied. These results are discussed in Chapter 5; Chapter 6 contains the conclusions and perspectives of this work.

### 3. Theory, measurements and models

#### 3.1. Theory

##### 3.1.1. Leaf-level CO<sub>2</sub> exchange and photosynthesis

Life on earth is enabled by the ability of vegetation to capture the energy of solar radiation and then convert it into chemical energy stored in the biomass. This process is called photosynthesis, and can be represented by a simple chemical equation:



Carbon dioxide and water molecules are transformed into carbohydrates and oxygen by solar energy. Even though the fundamental principle of photosynthesis is simple, it is in fact a very complicated phenomenon comprising many physical and biochemical processes. Some of the biochemical reaction chains still remain unknown (Lawlor, 1993).

The prerequisites for photosynthesis are radiation, the proper temperature, available water and carbon dioxide. The carbon dioxide needs to be transferred from the ambient air to the site of photosynthesis, the chloroplasts located in the mesophyll cells. First, a CO<sub>2</sub> molecule from the ambient air enters into the intercellular air space of the leaf through a stomatal pore. The guardian cells regulate the size of the stomatal opening according to the environmental conditions. The size of the aperture is described by the stomatal conductance. The definition of the stomatal conductance ( $g$ , unit  $\text{m s}^{-1}$ ) combines the flux ( $F$ , unit  $\text{mol m}^{-2} \text{s}^{-1}$ ) and the concentrations (unit  $\text{mol m}^{-3}$ ) in both the intercellular air space inside the leaf ( $c_i$ ) and outside ( $c_a$ ) the leaf. The flux, i.e., how much material moves across a surface in a certain time, is the difference between the inner and outer concentrations multiplied by the conductance:

$$F = g (c_a - c_i) \quad (2)$$

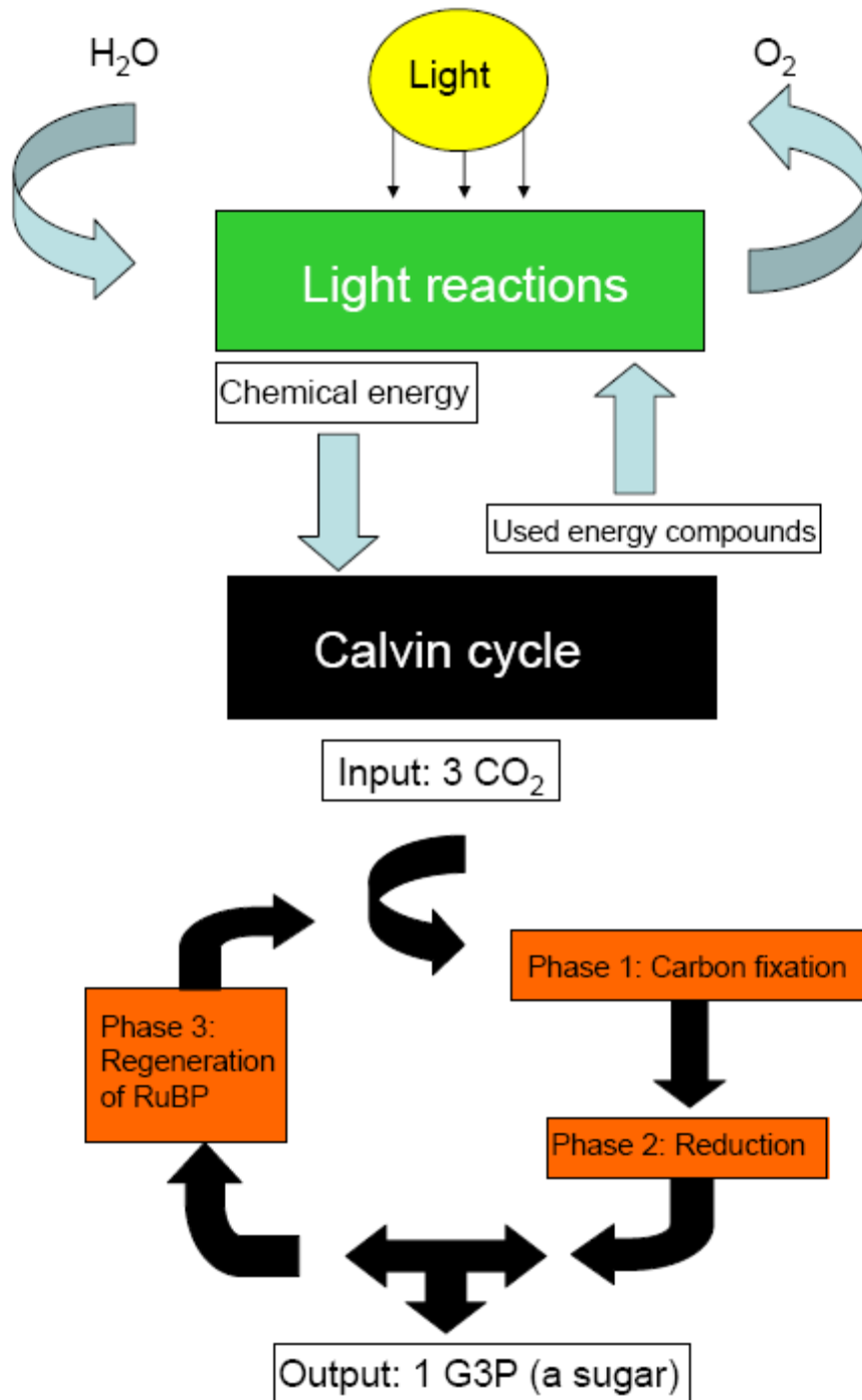


Figure 1. General picture of photosynthesis including light reactions and the three phases of the Calvin cycle. The light reactions use water and solar energy to create chemical energy compounds that are transported to the Calvin cycle. The three phases of the Calvin cycles use the chemical energy in reducing the  $CO_2$  molecules to a carbohydrate.

From the intercellular air the CO<sub>2</sub> molecules then diffuse into the mesophyll cells, inside which they are transported to the chloroplasts. The outer and inner membranes of the chloroplast enclose a fluid called the stroma. The stroma contains soluble enzymes, ribosomes and chloroplastic DNA. Interconnected thylakoid membranes segregate the stroma from another compartment, the thylakoid space. Chlorophyll and other photosynthetic pigments are located in the thylakoid membranes.

The photosynthesis consists of two stages, the light reactions and the Calvin cycle, also known as the dark reactions (Fig. 1). The light reactions take place in the thylakoid membrane and they convert light energy into chemical energy, NADPH and ATP (adenosine triphosphate) that are used in the Calvin cycle. NADPH is a reduced form of NADP<sup>+</sup>, nicotinamide adenine dinucleotide phosphate. An incoming light photon is trapped by photosynthetic pigments that transport the captured energy to a reaction centre, where chlorophyll-a is first excited and subsequently reduced by the primary electron acceptor. These photosynthetic pigments are parts of the so-called photosystems (Campbell and Reece, 2005).

Two types of photosystems work in the light reactions. Photosystem I (PSI) produces ATP, whereas photosystem II (PSII) and PSI together produce both ATP and NADPH. An electron transport chain from PSII to PSI involves, amongst other compounds, plastoquinone, and this electron flow also pushes electrons from water to NADPH and releases O<sub>2</sub>. Two distinct pathways are needed, since the Calvin cycle consumes more ATP than NADPH (Stryer, 1995).

The Calvin cycle occurs in the stroma. Carbon enters the Calvin cycle in the form of CO<sub>2</sub> and exits as a carbohydrate, glyceraldehyde 3-phosphate (G3P). In order to produce this carbohydrate, three CO<sub>2</sub> molecules are needed simultaneously. The Calvin cycle can be considered to consist of three phases, shown in Fig. 1, into which the three CO<sub>2</sub> molecules enter. First, in *the carbon fixation phase*, each CO<sub>2</sub> molecule is attached to a five-carbon sugar, ribulose biphosphate (RuBP). The enzyme catalyzing this reaction is RuBP carboxylase/oxygenase (Rubisco). Light-induced increases in the pH and Mg<sup>2+</sup> level of the stroma are also important stimulants for the reaction. The products of this reaction are hydrolyzed and in the second phase, *the reduction phase*, these hydrolyzed products are reduced by chemical energy from NADPH and ATP into G3P molecules. The net gain of the Calvin cycle is one G3P, since the other five G3P compounds produced continue to the third phase, *the regeneration of the CO<sub>2</sub> acceptor (RuBP)*. This is usually limited by the supply of ATP and NADPH (Farquhar et al., 1980). ATP molecules convert five molecules of G3P into three molecules of RuBP which are again available to receive CO<sub>2</sub>. The molecule of G3P produced is further converted to glucose and other essential organic compounds. The plants store carbohydrates mainly as sucrose in the cytosol (liquid in the cells) and starch in the chloroplasts (Stryer, 1995). The carbohydrates are used in cellular respiration and in synthesizing, e.g., proteins, lipids and polysaccharide cellulose (Campbell and Reece, 2005).

Most of the CO<sub>2</sub> released by plants is produced by cellular respiration, also called dark respiration. Cellular respiration in mitochondria releases the energy of the photosynthesis products into the plant cells, and consumes about 50% of the organic compounds made by photosynthesis (Campbell and Reece, 2005). Dark respiration is decreased in the presence of light (Villar et al., 1994; Villar et al., 1995; Laisk and Loreto, 1996).

The enzyme Rubisco can also catalyze a competing oxygenase reaction that releases CO<sub>2</sub> and consumes O<sub>2</sub>, but does not produce any high-energy compounds. This process is called photorespiration (Foyer et al., 2009). The relative rates of RuBP carboxylation and oxygenation depend upon the concentrations of CO<sub>2</sub> and O<sub>2</sub> at the active site of the enzyme as well as on the Rubisco specificity factor that describes the preference for CO<sub>2</sub> over O<sub>2</sub>. The Rubisco specificity factor is in the range 60 to 100 for higher plants (Laisk and Loreto, 1996; Andersson, 2008). In normal atmospheric conditions, the rate of the carboxylase reaction in Rubisco is four times faster than the rate of the oxygenase reaction (Stryer, 1995). Photorespiration increases with light, large O<sub>2</sub> and small CO<sub>2</sub> concentrations (Lawlor, 1993; Nobel, 1999).

Prerequisites for photosynthesis include light, temperature, water and CO<sub>2</sub>. Because light is needed in the light reactions, it is essential for photosynthesis to occur. The light reactions create the energy compounds for the Calvin cycle; with increasing light levels photosynthesis also increases, until light saturation occurs. When the light saturation level is reached, photosynthesis is no longer limited by light but by the amount of CO<sub>2</sub> available for the dark reactions and the amount of Rubisco (Lawlor, 1993; Bonan, 2008b).

Both photosynthesis and cellular respiration are highly dependent on temperature. Generally the biological activity is low at low temperatures, increasing in a temperature range from above zero up to an optimum temperature, after which a decrease occurs (Lawlor, 1993; Bonan, 2008b). Plants that are acclimated to low temperatures may have higher photosynthetic rates at lower temperatures and a lower optimum temperature for photosynthesizing than plants grown in higher temperatures (Berry and Björkman, 1980). The plants acclimate their optimum temperature for photosynthesis, but the time it requires varies according to species, ontogeny and nutritional status (Kozłowski and Pallady, 1997). At temperatures above the optimum level, plants usually close their stomata, especially if they are water-stressed (Berry and Björkman, 1980). The biochemical reduction of photosynthesis at high temperatures is associated with changes in the properties of the thylakoid membranes, inactivation of the enzymes of photosynthetic carbon metabolism and a decrease in the amount of soluble leaf proteins as a result of denaturation (Berry and Björkman, 1980).

CO<sub>2</sub> is also needed in the photosynthesis. Photosynthesis increases with increasing CO<sub>2</sub> concentration up to a certain saturation point. After that, the photosynthesis is limited by the ATP and NADPH supply from the light reactions (Lawlor, 1993; Bonan, 2008b). Nitrogen is an important component of chlorophyll and Rubisco, and higher amounts of nitrogen in foliage allow higher rates of photosynthesis (Bonan, 2008b).

### 3.1.2. Canopy-level CO<sub>2</sub> exchange

As plants photosynthesize, they produce organic compounds that are also referred to as gross primary production (GPP) ( $\text{mol m}^{-2} \text{s}^{-1}$ ) (Waring and Running, 2007). The cellular respiration of the plants is called autotrophic respiration ( $R_a$ ); when this is subtracted from the GPP, the remaining photosynthetic products are called the net primary production (NPP). These compounds are stored or used for growth (Campbell and Reece, 2005).  $R_a$  can be considered to consist of two processes, maintenance and growth respiration. It is usually modelled with an exponential temperature response (Waring and Running, 2007).

In this work the ecosystem studied was a boreal coniferous forest. When moving from the leaf level to the canopy scale, there are more contributors to the CO<sub>2</sub> gas exchange than the photosynthesizing green needles. The branches, stems and roots of the trees also respire, while the understory vegetation of the forest both photosynthesizes and respire.

The incoming litter from trees and dead plant material is decomposed by fungi, bacteria and soil animals, which thus release CO<sub>2</sub> into the atmosphere; this process is called heterotrophic soil respiration (Paul and Clark, 1989). Rhizospheric respiration also takes place in the soil and is a significant source of CO<sub>2</sub> (Kuzyakov and Cheng, 2001). It includes respiration by roots and their associated micro-organisms that are directly dependent on root exudates. In this work, rhizospheric respiration and heterotrophic respiration together form soil respiration ( $R_s$ ).

The heterotrophic soil respiration is dependent on various different environmental variables, temperature (Davidson and Janssens, 2006) and soil moisture (Moore and Dalva, 1993) being the most important, as well as the quality and supply of decomposable substrate material (Trumbore, 2006). The acidity of the soil also affects the activity of the enzymes that the microbes use in decomposition (Hari and Kulmala, 2009). The oxidation of photosynthetic products by soil microorganisms transform those products into nutrients that become available to plants and microorganisms (Paul and Clark, 1989). Soil microbes are able to decompose complex compounds because they produce complex enzyme systems, growing as communities that produce many different enzymes (Hari and Kulmala, 2009).

The temperature dependence of heterotrophic soil respiration can be described in several ways, including different exponential, e.g., van't Hoff, Arrhenius and Lloyd-Taylor as well as Gaussian formulations (Portner et al., 2009). Tuomi et al. (2008) showed that the Gaussian temperature dependence gives the best results for heterotrophic respiration from incubation experiments. Portner et al. (2009) argued that the Gaussian temperature dependence is often inadequate since it requires a reduction in released CO<sub>2</sub> at high temperatures, and often this is not seen in measurements. They found the second-best option to be the Lloyd-Taylor (Lloyd and Taylor, 1994) temperature dependence for heterotrophic respiration.

In addition to these biological processes for the release and uptake of CO<sub>2</sub>, various different physical transport mechanisms for the gases need to be considered when studying the gas exchange of the forest canopy. Inside the leaf, in the intercellular air space, and in the



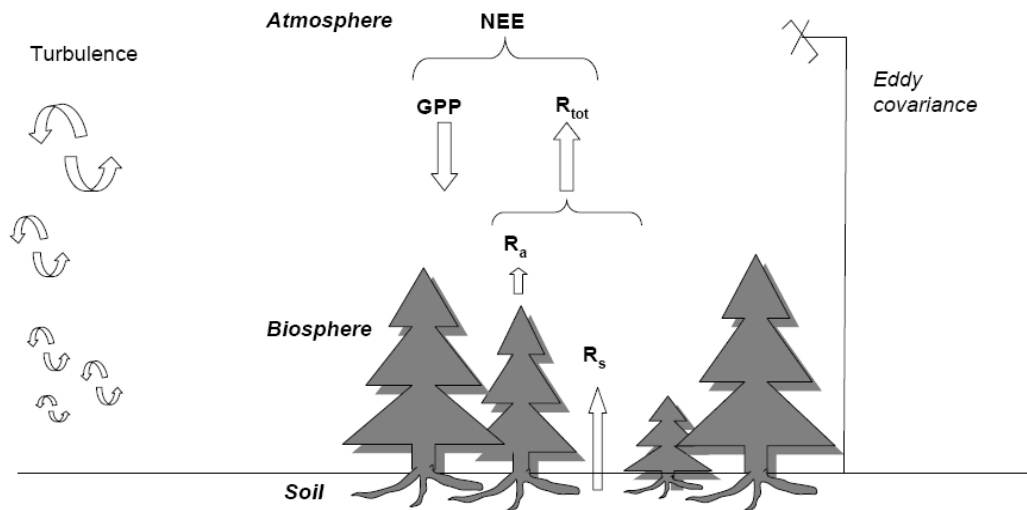


Figure 2. The  $\text{CO}_2$  fluxes of the forest.  $R_a$  refers to the autotrophic respiration of the biomass located above ground. [Picture adapted from A. Lohila (2008)].

laminar boundary layer, located within a distance of about 1 mm from the leaf surface in typical flow conditions, the gas molecules move by diffusion. Inside the canopy and within the atmospheric surface layer (ASL) the  $\text{CO}_2$  is transported by turbulence. The ASL is the approximately lowest 10% of the atmospheric boundary layer (ABL) and the ABL is the lower part of the troposphere (Stull, 1988). ABL is the part of the troposphere that is directly influenced by the earth's surface and ASL is a well-mixed layer within which all the fluxes are rather constant with height (Stull, 1988). The surface causes vertical mixing into the ASL by friction (mechanical turbulence) and heating (thermal turbulence), inducing swirls that are often referred to as turbulent eddies (Stull, 1988).

The fact that vertical fluxes within the ASL can be considered constant above the canopy (Stull, 1988) is used in micrometeorological measurements in which the forest  $\text{CO}_2$  exchange can be measured directly above the canopy using a three-dimensional wind component and  $\text{CO}_2$  concentration data. This method is called eddy covariance and the measured  $\text{CO}_2$  flux is called the net ecosystem exchange (NEE); it is the end result of all the  $\text{CO}_2$  exchange processes of the forest. In this work, the  $\text{CO}_2$  absorbed by the vegetation is considered negative and the  $\text{CO}_2$  flux directed upwards, i.e., the  $\text{CO}_2$  released by the vegetation, is positive. As described in the previous section, the dark respiration by the needles is decreased in light and photorespiration is increased with increasing  $\text{CO}_2$  assimilation. However, the respiration by the needles is not a very important part of the respiration of the whole forest. In a Scots pine forest in Zotino, the needle respiration accounted for 18% of the whole respiration budget (Shibistova et al., 2002). Thus the

photorespiration by the vegetation in the daytime can be considered negligible and the gross photosynthesis equals GPP. NEE can thus be formulated as

$$NEE = GPP - R_a - R_s = NPP - R_s \quad (3)$$

During the night, photosynthesis ceases and only respiration fluxes are present. NEE and the CO<sub>2</sub> fluxes it consists of are shown in Fig. 2.

### *3.1.3. Seasonality of the boreal forest*

Boreal forest covers approximately 14.5% of the earth's surface. It forms an almost uniform belt circling the land areas of the globe in northern latitudes, the largest continuous area extending from Scandinavia to eastern Siberia (Gower et al., 2001), covering most parts of Finland and Sweden. In boreal forests the winter is long, and the vegetation needs to make good use of the short summer period.

Winter time is harsh in the boreal region. To protect themselves, coniferous trees enter a dormant period, thus decreasing their need for assimilates. Mechanisms of survival include changes in energy absorption and photochemical transformation through energy partitioning, as well as changes in chloroplastic carbon metabolism and allocation (Ensminger et al., 2006). Also stomata close (Schaberg et al., 1995), and even wax-like plugs have been found in Scots pine needles in February in Siberia, probably protecting the trees from frost desiccation (Arneth et al., 2006). However, the plants are able to photosynthesize even during winter when the air temperature is high enough (Ensminger et al., 2004; Sevanto et al., 2006).

In northern latitudes in springtime, light is abundant even though the soil is still frozen. If plants were to open their stomatal pores and photosynthesize, they would desiccate (Arneth et al., 2006). The active xanthophyll cycle pigments protect the plants from the high light levels. In a Siberian Scots pine forest, the highest levels of xanthophylls were measured in April when it was still cold but the ambient light was already plentiful, not during the coldest time of the winter (Ensminger et al., 2004). In the same study it was observed that late night frosts not only halt, but even reverse, the biochemical recovery of the plants. Cold soils also slow the return of photosynthesis (Ensminger et al., 2008) and frozen soil inhibits the plants from obtaining soil water. Photosynthesis begins fully when the temperature is high enough and soil water is available.

Summertime is a time of growth in the boreal forest. Drought is not a seriously limiting factor in boreal forests, unlike in more southern ecosystems (Taiz and Zeiger, 1998). Some decrease in daily CO<sub>2</sub> exchange has been observed in boreal Scots pine forests on hot and dry days in Finland and Siberia (Kellomäki and Wang, 2000; Lloyd et al., 2002), but these studies did not report any extensive damage to the vegetation.

After a short summer, falling temperatures and decreasing day length drive plants to prepare for the winter and dormancy (Suni et al., 2003; Lagergren et al., 2008). The photosynthetic capacity of the boreal forests decreases (Lloyd et al., 2002) as the evergreen trees

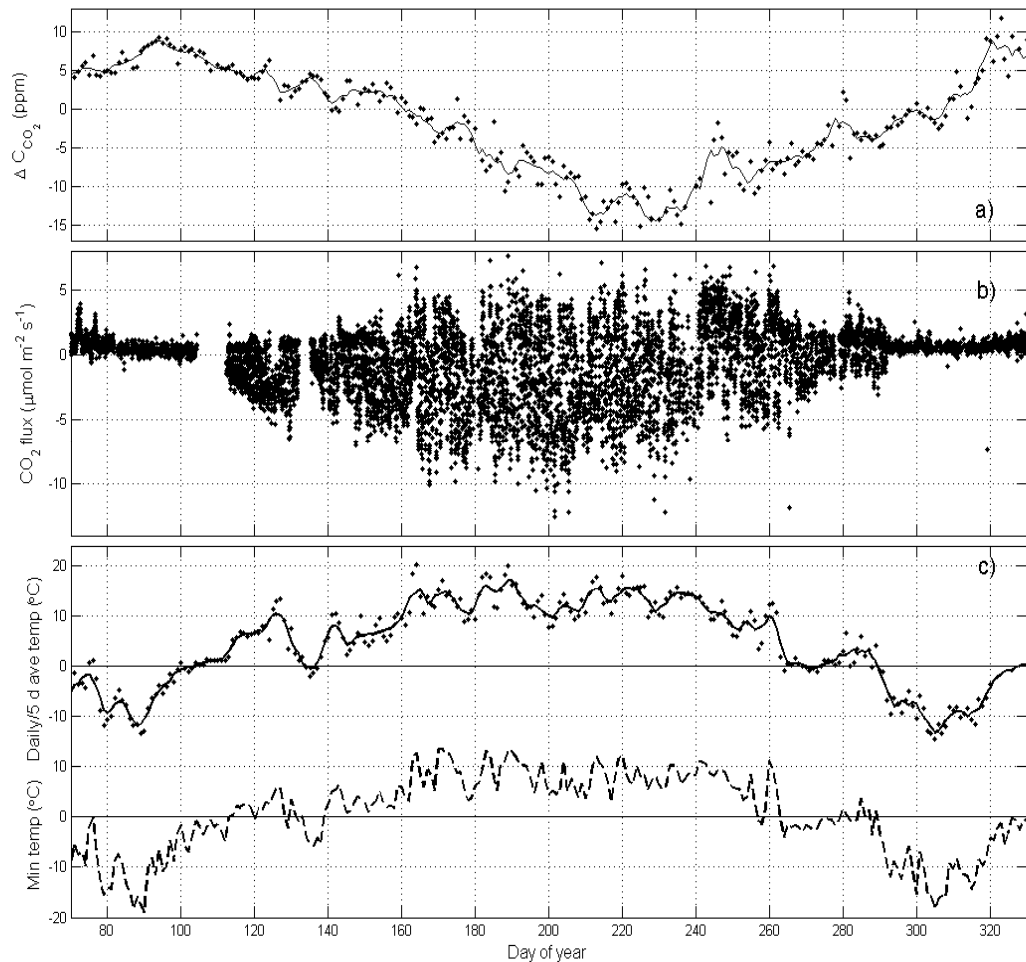


Figure 3.  $\text{CO}_2$  concentrations, fluxes and temperature indices at Pallas during the period March 11–November 26 (DOY 70–330) 2006. a) The five-day running average of trend-removed  $\text{CO}_2$  concentration at Pallas/Sammaltunturi (solid line) and the daily averages (points). b) The half-hourly eddy covariance  $\text{CO}_2$  fluxes from Pallas/Kenttäröva. c) Daily temperature (points), five-day running average of daily mean temperature (solid line) and minimum daily temperature (dashed line) for Pallas/Kenttäröva in 2006 (**Paper IV**).

downregulate their photosynthesis (Ensminger et al., 2006). They do this by inactivating the PSII reaction centres and by reorganizing the light-harvesting complexes efficient in light harvesting into complexes aimed at energy quenching (Öquist and Huner, 2003; Ensminger et al., 2006). Coniferous trees also increase the intercellular sugar concentration that increases their cold tolerance (Ögren, 1997).

A representative example of a typical seasonal cycle of a northern boreal coniferous forest is displayed in Fig. 3 showing  $\text{CO}_2$  gas exchange data, temperature indices and  $\text{CO}_2$  concentration measurements at Pallas/Kenttäröva, a Norway spruce forest located in northern Finland, in the year 2006 (see also **Paper IV**). Seasonal behaviour is also seen in

the CO<sub>2</sub> concentration, measured at Sammaltunturi, six kilometres away from Kenttäröva. There is a decrease from the winter level to the summertime minimum levels occurring in late July and early August (Fig. 3a). The CO<sub>2</sub> concentration results from a larger-scale phenomenon than the canopy-level measurement (Denning et al., 2003) and describes the general development in the region. A similar seasonal cycle is seen in the NEE measurements of the forest canopy (Fig. 3b). As the five-day average temperatures increase above zero in spring, the forest starts to take up carbon (Fig. 3c). Night frosts occurring before DOY 140 (May 20) in that year's spring decreased the uptake values, but shortly after this the spring recovery continued. Both uptake and respiration are at their highest levels during the summertime. In 2006, after DOY 240, in September, the maximum values start to decrease, slowly falling to their winter levels.

As can be seen in Fig. 3, the CO<sub>2</sub> gas exchange of the vegetation is closely linked to air temperature. Traditionally, the thermal growing season has been used to estimate the active period of the vegetation. The start of the thermal growing season occurs when the daily average temperature exceeds 5 °C on five consecutive days and the snow cover is absent, and ends when the average daily temperature is less than 5 °C on five consecutive days (Venäläinen and Nordlund, 1988). The temperature sum, i.e., the sum of all positive daily average temperatures, is also traditionally used (Solantie, 2004).

Recently, other temperature-related indices have also been developed to describe the vegetation's photochemical status. The seasonal factor (*f*) has a low value in the winter, increasing to a high summertime value in the spring (Lagergren et al., 2005). This increase is driven by air temperature, while night frosts cause some decrease in the value. In the autumn, the decrease is caused by diminishing day length and night frosts. The state of acclimation (*S*) is another temperature index that is used to describe seasonality; it follows temperature with a certain delay (Mäkelä et al., 2004). Tanja et al. (2003) showed the applicability of the five-day average temperature to estimate the beginning of the growing season.

The beginning of the snow melt in the spring can be seen as changes in the surface albedo (Kimball et al., 2004). The beginning of snow melt releases water into the top layers of the soil, thus enabling the trees to photosynthesize (Jarvis and Linder, 2000; Monson et al., 2002). The surface albedo decreases from its highest winter value to low summer values in spring as the snow melt advances. This occurs simultaneously as increasing temperatures drive other processes of spring recovery in the forest.

Chlorophyll fluorescence is a basic measurement in plant physiology (Baker, 2008). The light energy absorbed by the chlorophyll molecules is used in photosynthesis, dissipated as heat or re-emitted as light through chlorophyll fluorescence (Maxwell and Johnson, 2000). By measuring the chlorophyll fluorescence, information about these two simultaneous processes, i.e., photosynthesis and heat dissipation, is obtained.

The chlorophyll fluorescence parameter that is used is the maximum photochemical efficiency  $F_v/F_m$ , and is measured on a dark-acclimated leaf sample. The ratio  $F_v/F_m$  does not have units, and  $F_0$  (minimal fluorescence) and  $F_m$  (maximal fluorescence) that are used

in its calculation have only relative units (r.u.), since the measurement device relates the incoming signal to the signal it sends to the leaf sample. The minimum fluorescence  $F_0$  is measured first using a weak measuring beam, so that plastoquinone  $Q_A$  remains oxidized. The plastoquinone  $Q_A$  is the primary quinone electron acceptor of PSII. A short light flash is then applied and the level of the maximum fluorescence  $F_m$  is obtained. The light flash closes all the reaction centres, since once PSII absorbs light,  $Q_A$  is reduced - it is called 'closed' - and cannot accept a new electron before the first electron is passed to a subsequent electron carrier (Maxwell and Johnson, 2000; Baker, 2008). The maximum photochemical efficiency ( $F_v/F_m$ ) is calculated using  $F_0$  and  $F_m$ ,

$$F_v / F_m = \frac{F_m - F_0}{F_m} \quad (4)$$

$F_v/F_m$  gives information about the PSII functioning, and has a clear seasonal cycle in boreal forest, being low during winter and increasing to its highest level of 0.83 in summer. Its values in nonstressed leaves are consistent (about 0.83) (Baker, 2008). Seasonal changes in the value of  $F_v/F_m$  are driven by temperature and the light environment (Lundmark et al., 1998; Porcar-Castell et al., 2008a). These changes are caused by photochemical capacity, thermal dissipation of PSII, or both (Porcar-Castell et al., 2008b). The change in the surface albedo and the maximum photochemical efficiency  $F_v/F_m$  in spring 2002 at Sodankylä are shown in Fig. 4; they are a typical example of the spring recovery in a boreal forest. The albedo decreases simultaneously as  $F_v/F_m$  increases to the summer level during spring, large changes occurring quite rapidly.

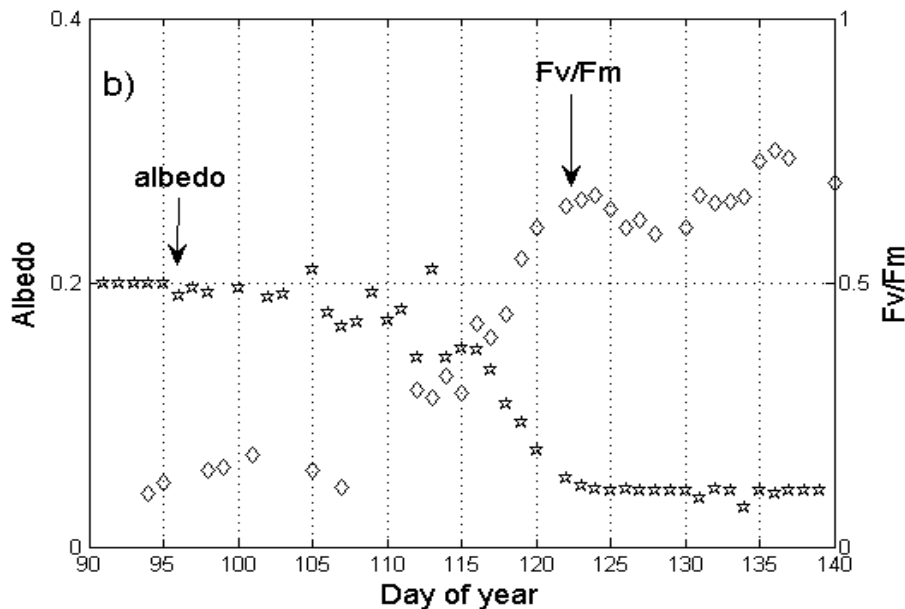


Figure 4. Maximum photochemical efficiency  $F_v/F_m$  (diamonds) and albedo (stars) at Sodankylä in spring 2002 (March 31 – May 20).

## 3.2. Model description

### 3.2.1. The biochemical model

To study the CO<sub>2</sub> gas exchange of the plants, leaf-level photosynthesis models were used. The biochemical model was developed in the early 1980's by Farquhar and co-workers (Farquhar et al., 1980; Farquhar and von Caemmerer, 1982). It has been later modified by De Pury and Farquhar (1997). The model is based on a description of photosynthesis at the chloroplast level including enzyme kinematics and biochemistry. It has been widely used in photosynthesis models, from leaf to global scales (Sellers et al., 1996; Friedlingstein et al., 2006). According to the biochemical model, photosynthesis is limited by the electron transport chain ( $A_j$ , RuBP regeneration-limited) or carboxylation efficiency ( $A_c$ , Rubisco activity-limited). Some versions of the model also consider nutrient limitation (Dang et al., 1998), but that was excluded in this work. One or other rates of synthesis ( $A_j$  or  $A_c$ ) are thus limiting values and the net CO<sub>2</sub> gas exchange ( $E$ ) can be formulated as:

$$E = \min\{A_j, A_c\} - R_d \quad (5)$$

where  $R_d$  is the rate of cellular non-photorespiratory respiration.

When the leaf-level photosynthesis is limited by the Rubisco activity, it is denoted by  $A_c$ . This occurs at high light levels or when the CO<sub>2</sub> concentration is low, and it is described as

$$A_c = V_{c(\max)} \frac{c_i - \Gamma^*}{k_c (1 + o/k_o) + c_i} \quad (6)$$

Here  $V_{c(\max)}$  is the maximum rate of carboxylation,  $k_c$  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 the chloroplasts (assumed constant) and  $c_i$  is the carbon dioxide concentration inside the chloroplasts.

RuBP regeneration-limited CO<sub>2</sub> gas exchange is denoted by  $A_j$  and is dominant at low light levels or when the CO<sub>2</sub> concentration is high. Its formulation is

$$A_j = J \frac{c_i - \Gamma^*}{4(c_i + 2\Gamma^*)} \quad (7)$$

In addition to the variables introduced above, eq. (7) includes  $J$ , the potential electron transport rate that is described as

$$J = \frac{qI_o + J_{\max} - \sqrt{(qI_o + J_{\max})^2 - 4\Theta qI_o J_{\max}}}{2\Theta} \quad (8)$$

It is a function of the incident irradiance ( $I_0$ ), the light use efficiency factor ( $q$ ), the convexity of the light response curve ( $\Theta$ ) and  $J_{max}$ , the maximum rate of electron transport.

The temperature dependence for  $\Gamma^*$  was adopted from Brooks and Farquhar (1985), while the temperature dependences for the Michaelis-Menten constants were from Farquhar et al. (1980) and Harley and Baldocchi (1995). The temperature dependence of  $V_{c(max)}$  and  $J_{max}$  for some species can be presented according to Harley and Baldocchi (1995) as:

$$f_T = f_0 \exp\left[\frac{E_f(T - T_{25})}{T_{25}RT}\right] \quad (9)$$

where  $f_0$  is the base rate, denoting the parameter value at 25 °C,  $E_f$  is the activation energy,  $R$  is the gas constant,  $T$  is temperature (K) and  $T_{25}$  is 298.15 K.

The temperature dependence of  $J_{max}$  can also be described by a function revealing an optimum temperature (Farquhar et al., 1980; Medlyn et al., 2002a):

$$J_{max} = \frac{B \exp\left(\frac{E_j(T/T_{25} - 1)}{RT}\right)}{1 + \exp\left(\frac{S_j T - H_j}{RT}\right)} \quad (10)$$

Here  $E_j$  is the activation energy,  $S_j$  is the entropy of the denaturation equilibrium,  $H_j$  is the deactivation energy for  $J_{max}$ ,  $T$  is temperature (K),  $R$  is the gas constant and  $B$  is a constant having the same units as  $J_{max}$ .  $T_{25}$  is 298.15 K. This formulation for  $J_{max}$  was used in **Paper I**.

The parameters  $J_{max}$  and  $V_{c(max)}$  can be estimated from leaf chamber measurements (Wang et al., 1996; Aalto and Juurola, 2001). The parameters cannot be measured directly but they must be inferred by model inversion from measurements (Kattge et al., 2009). In addition to the parameterizations at leaf level, model inversions using eddy covariance data have also been made to estimate the model parameters at canopy level and on terrestrial ecosystem models (Knorr and Kattge, 2005; Wang et al., 2006; **Paper III**).

Earlier these parameters were considered to be highly variable between plants (Farquhar et al., 1980; Wullschleger, 1993), with differences originating from genotype, nutrition, etc. However, Leuning (2002) showed that these parameters have similar temperature dependences between species at temperatures below 30 °C. In a study where different measurements were compared, Medlyn et al. (2002a) found that the relative temperature responses of  $J_{max}$  and  $V_{c(max)}$  were fairly stable among tree species. Kattge et al. (2009) were able to parameterize  $V_{c(max)}$  globally according to the plant functional types. The large differences in the values measured earlier (Wullschleger, 1993) resulted from different experimental conditions and special characteristics. Even though parameterization for the

large scale has been successful, noticeable differences within species have been found (Medlyn et al., 1999).

In Finland, the biochemical model parameters have been found to have a seasonal behaviour (Wang, 1996). This has also been noticed in other studies (Wilson et al., 2001; Xu and Baldocchi, 2003; Kosugi and Matsuo, 2006). The parameter  $V_{c(max)}$  has been shown to vary with nitrogen (Medlyn et al., 1999), and this has been used in parameterizations (Kellomäki and Wang, 2000; Kattge et al., 2009). The acclimation to plant growth temperature has also been taken into account in parameterization (Kattge and Knorr, 2007). The relations to nitrogen and plant growth temperature were not considered in this study, only the seasonal behaviour.

The biochemical model does not contain any formulation for stomatal conductance. The widely-used Ball-Berry conductance model (Ball et al., 1987) was used in conjunction with the biochemical model. The stomatal conductance  $g_{BB}$  is formulated as

$$g_{BB} = g_0 + g_1 \frac{H_r A}{c_a} \quad (11)$$

where  $H_r$  is the relative humidity,  $A$  is the rate of photosynthesis,  $c_a$  is the ambient CO<sub>2</sub> concentration and  $g_0$  and  $g_1$  are empirical constants. The empirical constants  $g_0$  and  $g_1$  were approximated using eddy covariance and leaf chamber data measured at the Sodankylä Scots pine site (**Paper II**). The stomatal conductance model parameters also change seasonally (Medlyn et al., 2002b). The effect of drought or increased vapour pressure deficit (VPD) can be simulated by the Ball-Berry model with a modification proposed by Tuzet et al. (2003), where the second term on the right-hand side of eq. (11) is multiplied by a sigmoid function that decreases as a function of increasing VPD.

### 3.2.2. Optimal stomatal control model

Another leaf-level photosynthesis model used in this work was an optimal stomatal control model. In 1977 Ian Cowan argued, that plants optimize the amount of transpired water to the amount of produced carbohydrates under prevailing environmental conditions (Cowan, 1977). This principle has been further developed into a photosynthesis model also including a formulation for stomatal conductance (Hari et al., 1986; Mäkelä et al., 1996). The photosynthesis  $A_o$  is described as

$$A_o(t) = \frac{(g(t)C_a + r)f(I(t))}{g(t) + f(I(t))} \quad (12)$$

where  $C_a$  is the ambient CO<sub>2</sub> concentration,  $r$  is the cellular respiration rate and  $g$  is the conductance.

The saturation of the biochemical reactions is represented by a function  $f$  of irradiance ( $I$ ):



$$f(I) = \frac{\beta I}{I + \gamma}. \quad (13)$$

Here  $\gamma$  represents the function's convexity and  $\beta$  is a parameter describing the photosynthetic capacity.

The stomatal conductance  $g$  is included in the model, and is described as

$$g = \left( \sqrt{\frac{C_a - (r / f(I(t)))}{\lambda a D(t)}} - 1 \right) f(I(t)) \quad (14)$$

where  $\lambda$  is the cost of transpiration,  $D$  is the saturation deficit of water vapour and  $a$  is the ratio of the diffusivity of water vapour to that of  $\text{CO}_2$ . The parameters  $\lambda$  and  $\gamma$  were assumed to remain constant during the growing season, and were adopted from the leaf chamber measurements at Värriö, as described by Hari and Mäkelä (2003). The parameter  $\beta$  was determined from the eddy covariance data in **Paper II**. This model has been successfully applied at both the leaf (Hari et al., 1999; Hari et al., 2000) and canopy levels (Hollinger et al., 1998).

### 3.2.3. Upscaling the leaf-level models

To simulate the  $\text{CO}_2$  gas exchange of the whole canopy, the leaf-level models need to be up-scaled (**Paper II**; **Paper III**). In a forest canopy more processes are involved than just those at the leaf level. The radiation and temperature are distributed unevenly inside the forest canopy, the woody parts of tree respire and the vegetation at the forest floor photosynthesizes and respire. Microbes in the soil release  $\text{CO}_2$  from the soil, thus causing heterotrophic respiration.

When modelling the forest canopy, various alternatives are available: the canopy can be considered to consist of one layer, i.e., the so-called big-leaf approach, the biomass can be divided into multiple layers (De Pury and Farquhar, 1997) or the canopy structure can be considered to consist of individual crowns in two or three dimensions (Medlyn et al., 2005a; Mäkelä et al., 2006). In this work, the multilayer approach was used, since it facilitates the description of the vertically-changing efficiency of the biochemical model parameters and varying light levels inside the canopy. To describe the vertical profile of the biomass distribution for Scots pine, a beta distribution was used (Wu et al., 2003). We divided the vertical profile into four parts, each of which had about a quarter of the total leaf area.

The two-stream approximation radiative transfer model (Sellers, 1985) was used to calculate the radiative transfer inside the canopy. This model calculates the radiative fluxes separately for direct and diffuse radiation and allows for multiple reflection of light by leaves (Sellers et al., 1986). To estimate canopy respiration, soil and foliar respirations were considered. Foliar respiration was estimated from the leaf chamber measurements, and a Lloyd-Taylor (1994) temperature dependence was fitted to it. Night-time eddy covariance measurements

were used to estimate soil respiration. Bi-weekly changing temperature fits (Lloyd and Taylor, 1994) to measurement data were made (**Papers II and III**).

The photosynthesis parameters  $J_{max}$  and  $V_{c(max)}$  of the biochemical model were assumed to decrease proportionally to the percentual PAR (Photosynthetically Active Radiation) (Kull and Jarvis, 1995; Sellers et al., 1992), when upscaling the model in multiple layers. In the biochemical model, calculations were made separately for the sunlit and shaded leaves of the canopy (Thornley, 2002).

#### 3.2.4. Three-dimensional (3-D) leaf model

Aalto and Juurola (2002) have presented a 3-D model for a silver birch leaf (lat. *Betula Pendula*) that describes a single stoma in a very detailed manner. The model includes the leaf boundary layer, the stomatal opening, the intercellular air spaces, the palisade and spongy mesophyll cells and individual chloroplasts. Physical transport processes are described in the model. The CO<sub>2</sub> molecule moves through the laminar boundary layer and stomatal opening into the intercellular air space by diffusion. It then enters the mesophyll cell; this discontinuous jump between an air space and a liquid cell is described by Henry's law that provides a temperature-dependent absorption equilibrium constant. Inside the mesophyll cells, the CO<sub>2</sub> molecules move by diffusion into the chloroplasts. The light attenuation inside the leaf is modelled by Beer's law (Lloyd et al., 1992). The strength of the chloroplast sink is determined by the biochemical photosynthesis model, depending on the local environmental conditions. The photosynthesis parameters for the model,  $J_{max}$  and  $V_{c(max)}$ , have been estimated earlier for silver birch by laboratory leaf gas exchange measurements (Aalto and Juurola, 2001).

### 3.3. Measurements

This work used CO<sub>2</sub> gas exchange measurements from four different eddy covariance sites located in Finland and Sweden. In addition, leaf chamber CO<sub>2</sub> gas exchange and chlorophyll fluorescence measurements from Finnish Lapland were used, as well as CO<sub>2</sub> concentration measurements.

#### 3.3.1. Measurement sites

The micrometeorological CO<sub>2</sub> measurements used in this work were made at four coniferous forest sites, all located in the boreal zone: Kenttäröva, Sodankylä, Hyytiälä and Norunda. The Scots pine forest at Sodankylä is located within the Arctic Research Centre of the Finnish Meteorological Institute and leaf chamber CO<sub>2</sub> exchange and chlorophyll fluorescence measurements were also made there. Kenttäröva and Sodankylä are both located north of the Arctic Circle in the north boreal zone (Solantie, 1990), while Hyytiälä is in southern Finland in south boreal zone. Norunda is located in the hemi-boreal zone in the central part of Sweden.

The spruce forest of Kenttäröva is located at Pallas, six kilometres from Sammaltunturi, the site of the CO<sub>2</sub> concentration measurements. The Sammaltunturi measurement station is

located on the treeless top of an arctic hill, 560 m above sea level and 300 m above the surroundings (Aalto et al., 2002). The forest site at Pallas will hereafter be referred to as Pallas/Kenttäröva and the CO<sub>2</sub> concentration measurement site as Pallas/Sammaltunturi. The locations of the measurement sites are shown in Fig. 5, while basic information about the sites is found in Table 1.

### 3.3.2. Leaf chamber CO<sub>2</sub> measurements

The gas exchange of tree twigs is measured using leaf chambers. A twig refers to the branch of a tree with its needles or leaves attached. A twig is placed in a chamber and the concentrations of CO<sub>2</sub> and water vapour together with the environmental conditions are observed. The leaf chamber measurements can either be made in a closed setup, when there is no incoming air entering the chamber, or else in a steady state with a constant air flow through the chamber. Studies using leaf chambers are common, and have been done in Finland on Scots pine shoots by, e.g., Wang et al. (1996), Aalto (1998) and Kolari et al. (2007) and on birch leaves by, e.g., Hari and Luukkanen (1974).

In this work the leaf gas exchange was measured at Sodankylä in the spring and summer of 2002 with an LI-6400 (LiCor Inc., USA), a portable open-system leaf chamber measurement device. Experiments with different light levels and CO<sub>2</sub> concentrations in a steady state were made, and these data were used to determine the needle respiration and photosynthesis model parameters.

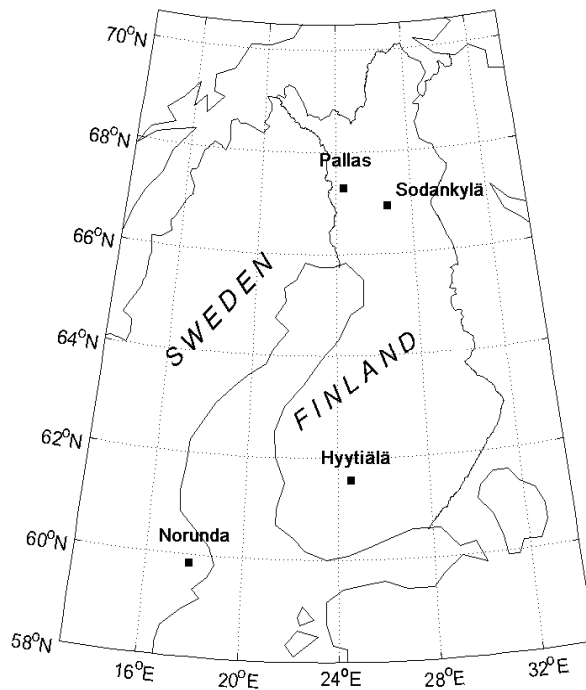


Figure 5. Locations of the measurement sites.

### 3.3.3. Eddy covariance measurements

CO<sub>2</sub> and H<sub>2</sub>O gas exchanges can be measured at the canopy level by the micrometeorological eddy covariance method. This is based on high-frequency observations of H<sub>2</sub>O and CO<sub>2</sub> concentrations and wind components that are together used to calculate the direct fluxes of H<sub>2</sub>O and CO<sub>2</sub> between the ecosystem and the atmosphere (Moncrieff et al., 2004). Such measurements are now performed world-wide in multiple locations, the longest time series having started in 1990 (Baldocchi, 2003). In Finland, long-term measurements have been carried out at Hyytiälä since 1996 (Vesala et al., 1998; Markkanen et al., 2001) and at Sodankylä since 2000 (Aurela, 2005).

The eddy covariance method measures NEE. A 30-minute time period is used in eddy covariance measurements, since this gives approximately the net amount of material being transported in the vertical direction above the surface (Aubinet et al., 2000). This is expected, since corresponding to this averaging time there is a gap in the energy spectrum of the wind speed at 0.1-1 h<sup>-1</sup> (Stull, 1988), but use of longer time periods has also been discussed (Finnigan et al., 2003).

Table 1. The characteristics of the micrometeorological measurements sites.

	Kenttäröva	Sodankylä	Hyytiälä	Norunda
Location	67°59'N 24°15'E	67°21'N 26°38'E	61°51'N 24°17'E	60°5'N 17°28'E
Forest type	Norway spruce	Scots pine	Scots pine/ Norway spruce	Scots pine/ Norway spruce
LAI (m <sup>2</sup> /m <sup>2</sup> ) (total, annual)	6.6	3.6	8.0 <sup>a)</sup>	13.5
Mean annual temperature (C°) and precipitation (mm) (30 year average)	-1.7 450	-1.0 500	3.0 709	5.5 527
Canopy height (m)	13	12	13	28
Measurement height (m)	23	23	23	35
References	b)	b)	c)	Grelle et al. 1999

<sup>a)</sup>Thinning in spring 2002 reduced LAI from 8 m<sup>2</sup>/m<sup>2</sup> to 6 m<sup>2</sup>/m<sup>2</sup>, after that a 0.3 m<sup>2</sup>/m<sup>2</sup> increase yearly (P. Kolari, pers. comm.)

<sup>b)</sup>Aurela (2005) and Finnish Meteorological Institute (1991)

<sup>c)</sup>Markkanen et al. 2001 and Vesala et al. 1998, 2005

The concentrations of H<sub>2</sub>O and CO<sub>2</sub> and the wind components were measured above the canopy level. EC measurements from four sites were used in this work; their canopy and measurement heights are shown in Table 1. Wind components were measured by a three-dimensional anemometer and trace gas concentrations by an infrared H<sub>2</sub>O/CO<sub>2</sub>-analyzer. At Sodankylä and Kenttäröva an LI-7000 was used as the CO<sub>2</sub>/H<sub>2</sub>O monitor and at Norunda and Hyytiälä an LI-6262 (Li-Cor Inc., NE, USA). The anemometers at Sodankylä and Kenttäröva were SATI/3Sx (Applied Technologies Inc., CO, USA) until 2003, after which they were replaced by METEK USA-1 instruments (METEK GmbH, Elmshorn, Germany). At Norunda and Hyytiälä, the anemometers were Gill Solent 1012-R2 (Gill Instruments Ltd, Lymington, UK).

The benefits of the EC method include the fact that it measures at canopy level, which is interesting for ecological studies (Baldocchi, 2003), and that it is continuous, allowing for studies of both short-term variations and annual carbon balances. In addition, the EC method does not disturb the environment or the vegetation (Aurela, 2005). The disadvantages include expense, as well as difficulties in making error estimations and defining the source area of the fluxes in heterogeneous landscapes (Markkanen et al., 2003). All single EC data values include a of random error between 10-20 % due to turbulent transport phenomena (Baldocchi, 2003; Rannik et al., 2004; Richardson et al., 2006) and systematic errors, caused by, e.g., data processing.

#### *3.3.4. Chlorophyll fluorescence measurements*

Since 2001 the maximum photochemical efficiency  $F_v/F_m$  has been measured at Sodankylä about twice a week. The needles are first dark-adapted by leaf clips. Measurements are taken from four trees that are located in a well-illuminated environment. During spring 2002 there was a measurement campaign at Sodankylä to capture the spring recovery of the forest using different chlorophyll fluorescence measurements together with CO<sub>2</sub> gas exchange and reflectance measurements (**Paper V**). The aim was to study whether measuring the sun light-induced fluorescence signal was possible at the canopy scale in a coniferous forest. Measurements were made both with an active detector, a lidar, and also with a passive detector based on the Fraunhofer line principle (Moya et al., 2004).

#### *3.3.5. CO<sub>2</sub> concentration measurements*

The atmospheric CO<sub>2</sub> concentration is measured globally in the Global Atmospheric Watch (GAW) network organized by the World Meteorological Organization (WMO). Continuous measurements of CO<sub>2</sub> concentration began at Pallas/Sammaltunturi in 1996. The measurement device was an LI-6252 infrared gas analyzer (Li-Cor Inc., NE, USA) that was calibrated every 2.5 hours using gases with known concentrations. These gases were calibrated every three months against WMO/CCL (NOAA/ESRL) standards on the WMO-2007 scale. The hourly CO<sub>2</sub> concentration is calculated as the mean of 12 sampling periods, each 1 minute long (Aalto et al., 2002). The accuracy of the measured CO<sub>2</sub> concentration is better than 0.1 ppm. The measurements are described in detail in Hatakka et al. (2003).

## 4. Results

This section contains the main results of this work. The 3-D leaf stomata model was used to study the temperature dependences of the biochemical model and how they differ from the temperature dependences found from the leaf chamber measurements (**Paper I**). In addition, two different photosynthesis models were upscaled to the canopy level and their results compared (**Paper II**). The upscaled biochemical model was used in data inversion to study the biochemical parameters (**Paper III**). Lastly, the seasonal cycle and the linkage between CO<sub>2</sub> gas exchange with environmental and biological variables was studied in coniferous forests (**Paper IV**).

### 4.1. Redefining the biochemical model parameters at leaf level

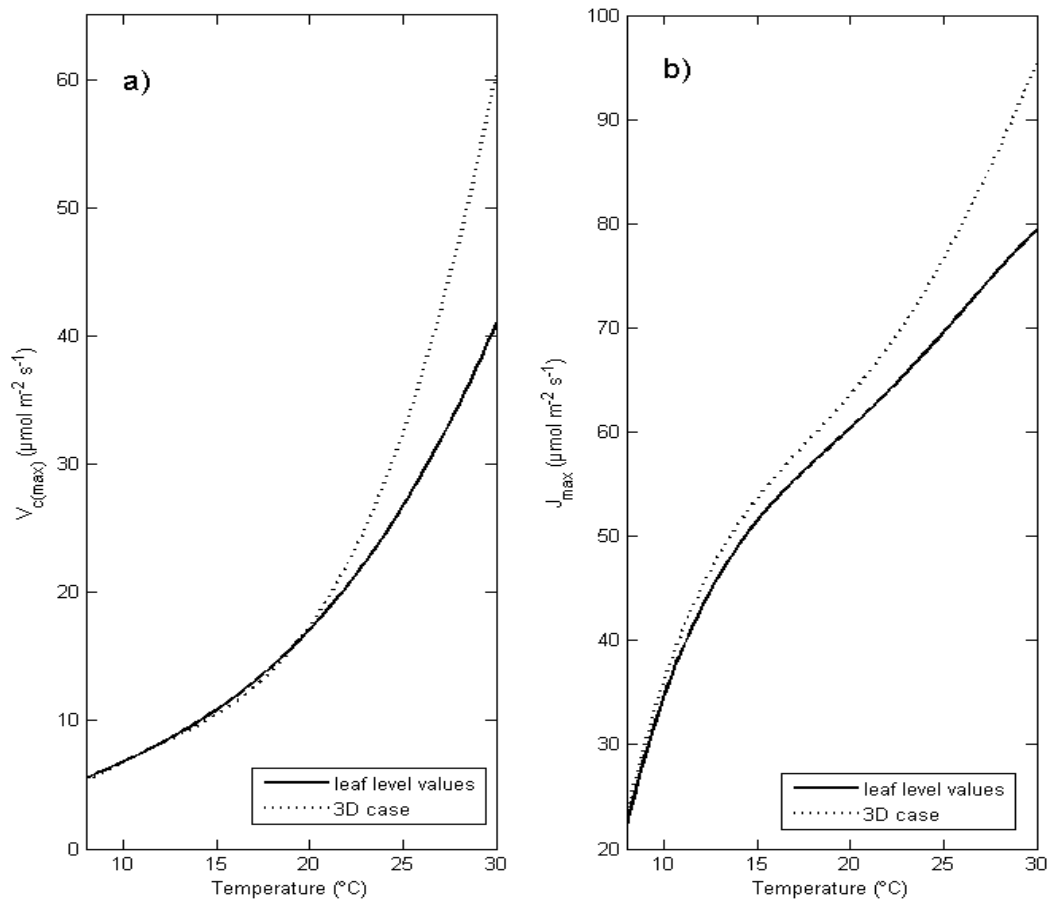
The 3-D stomata model for a birch leaf was used to study the role of physical processes in CO<sub>2</sub> gas exchange, and new chloroplastic temperature dependences for the biochemical model parameters  $V_{c(max)}$  and  $J_{max}$  were calculated (**Paper I**). Usually when the biochemical model is used, the intercellular CO<sub>2</sub> concentration is assumed to represent the chloroplastic CO<sub>2</sub> concentration, thus neglecting the mesophyll conductance describing the transport into the mesophyll cell, as well as the diffusion in the gas and liquid phases.

The CO<sub>2</sub> fluxes from the 1-D case and the 3-D case with the same biochemical parameters and environmental conditions were compared to assess the differences caused by the detailed 3-D model structure. The 3-D case had lower CO<sub>2</sub> fluxes, and this phenomenon was more pronounced at higher temperatures. This results from the dissolution phenomena at the mesophyll cell surface, the cumulative effect of leaf structure, diffusion in the liquid and the light environment inside the leaf. A sensitivity test was conducted to assess the relative significance of the different physical transport processes for the temperature dependence of the CO<sub>2</sub> exchange. Since the diffusion in the gas and liquid phases and the dissolution of CO<sub>2</sub> in water have different temperature dependences, their relative influences on the CO<sub>2</sub> exchange vary. The dissolution of CO<sub>2</sub> in water had a marked effect on the CO<sub>2</sub> exchange at high temperatures, while the diffusion in the liquid and gas phases had a lesser effect. However, the diffusion coefficient for the mesophyll was estimated to be the same as that of water, even though in reality it is most probably smaller, thus causing a larger limitation to the diffusion of CO<sub>2</sub>. The limitation to the dissolution of CO<sub>2</sub> described by Henry's law decreases with increasing temperature, causing a temperature optimum to occur in the CO<sub>2</sub> gas exchange at 22 °C in the 3-D case, while there was no temperature optimum in the 1-D case.

The temperature dependences for the biochemical parameters  $V_{c(max)}$  and  $J_{max}$  were re-estimated using the 3-D structure. The light attenuation inside the leaf had a substantial impact on the parameter values, and there was also a need to re-estimate the light use efficiency factor  $q$  so as to be able to estimate  $J_{max}$ . The temperature dependences of these newly-evaluated parameter values, as well as the values obtained from the leaf level measurements, are displayed in Fig. 6. The new chloroplastic parameters had larger values

at high temperatures than the original ones from the measurements, due to the CO<sub>2</sub> dissolution.

The model grid used in this study was made by accurately copying the stomata structure of the material used in the measurements, and the results are at least species specific. In conifers, the diffusion pathway inside the mesophyll cells is longer, and therefore the physical transport mechanisms might influence the temperature response of CO<sub>2</sub> gas exchange differently.



*Figure 6. The biochemical model parameters  $V_{c(max)}$  (a) and  $J_{max}$  (b) as a function of temperature. The solid line represents the values estimated from the leaf-level measurements using 1-D model, while the dotted line shows the values obtained using the 3-D model. The lines are polynomial approximations valid from 8 to 30 °C (Paper I).*

## 4.2. Comparison of results from two upscaled leaf-level models

The CO<sub>2</sub> gas exchange is often modelled with photosynthesis models developed at the leaf level. This represents a challenge when upscaling to the canopy level, since usually only the parameterization obtained from the leaf chamber measurements is used. The existence of eddy covariance data allows us access to continuous data at the canopy scale for multiple years.

Two distinct photosynthesis models were upscaled to the canopy level and parameterized using eddy covariance data at Sodankylä (**Paper II**). The photosynthesis models used were the biochemical model and the optimal stomatal control model, referred to hereafter as the OM model. These two models have different foundations, the first one being based on the biochemistry of chloroplasts, while the latter is based on an evolutionary optimisation argument. The object of this study was to address the differences between the models, to develop a good but simple way of upscaling the models and lastly, to parameterize the models by taking into account seasonality.

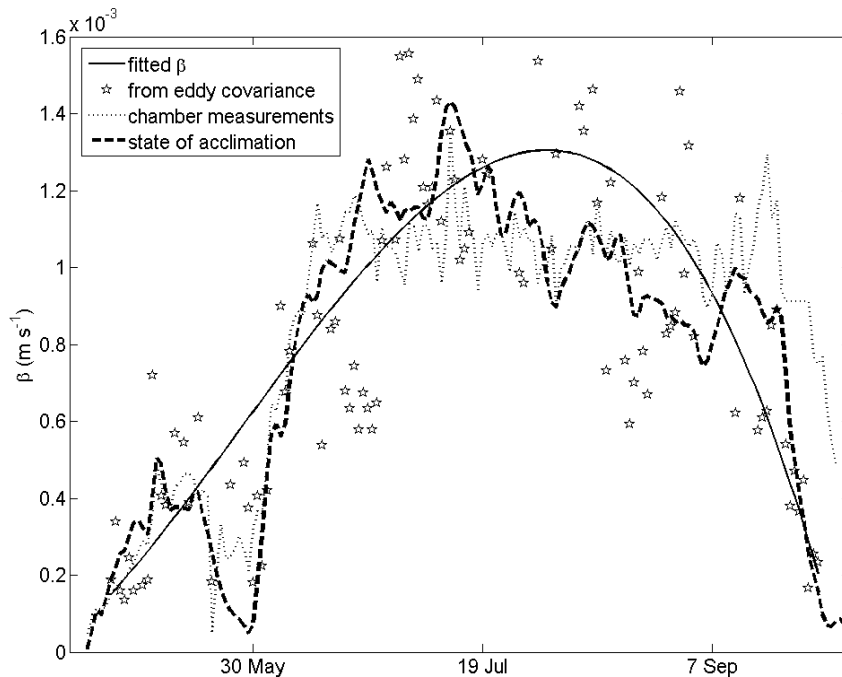


Figure 7. The scattered points denote values of  $\beta$  obtained from eddy covariance data inversion and the solid line is a polynomial fit to these points. The dotted line is the scaled  $\beta$  estimated from chamber measurements and the dashed line is the scaled state of acclimation (**Paper II**).



The OM model is simple to parameterize, since it has three parameters of which  $\beta$ , the photosynthetic capacity, changes seasonally, while the other two ( $\lambda$  and  $\gamma$ ) can be kept constant. When eddy covariance data was used in the parameterization, the daily values of  $\beta$  appeared to be quite scattered (**Paper II**). These inversed  $\beta$  values with a polynomial fit, together with chamber estimates for  $\beta$  as well as  $\beta$  estimated by the state of acclimation, a temperature-related index, are shown in Fig. 7. A polynomial fit having a parabolic behaviour and its maximum values at mid-summer was fitted to the inversed values. This fit simulated the CO<sub>2</sub> fluxes of the forest quite well, apart from some overestimation after some frost nights and on bright summer days. Chamber data from Värriö, another Scots pine site located at the same latitude as Sodankylä, was also employed to estimate  $\beta$ , but did not lead to better estimates. Instead, a temperature-related index, the state of acclimation, was enough to parameterize  $\beta$ , without any need to employ leaf chamber or eddy covariance data. This makes the OM model highly applicable. The OM model does not include a temperature dependence for photosynthesis, being driven by light and vapour pressure deficit. Its strength lies in the simple formulation that does not require complicated parameterization and in good performance, except with some overestimation of the CO<sub>2</sub> fluxes at high light levels.

The parameterization of the biochemical model is more challenging. The two different limiting CO<sub>2</sub> assimilation rates, RuBP regeneration-limited and the Rubisco activity-limited, both govern the CO<sub>2</sub> gas exchange simultaneously at different heights inside the canopy, depending on the light level. The strong temperature dependences of the parameters add to the difficulties. Many different approaches were tried and different upscaling procedures were experimented with to obtain a successful parameterization. The best results were obtained when seasonally-changing temperature dependences for the parameters were introduced. The fitting periods were determined by the magnitude of the inversed parameter values on the temperature response curve and the goodness of the simulated CO<sub>2</sub> fluxes. The parameter  $J_{max}$  had one temperature response fit for early summer, until June 3, and another for the rest of the summer (Fig. 8a). The parameter  $V_{c(max)}$  had one fit for spring (May 1 – June 3), one for early summer (June 4 – June 27) and one for the rest of the summer (Fig. 8b). Both activation energy and base rate in eq. (9) were allowed to change when these fittings were performed. The biochemical model also showed itself successful in simulating the CO<sub>2</sub> fluxes without any biases, thus being more promising than the OM model.

The magnitude of the parameter  $J_{max}$  was in accordance with the literature and chamber measurements at low temperatures, but was overestimated at high temperatures. The inversed  $V_{c(max)}$  values were close to the literature values. This implied that the ratio  $J_{max}/V_{c(max)}$  found was 3.9 at 17 °C in summertime, even though values close to 2 have been reported in the literature (Medlyn et al., 2002b).

The year 2001 was used to parameterize the models and the year 2002 was used as a test year to investigate the models' performance. The parameterization of the biochemical model proved to be inadequate in the warmer spring of 2002. Calendar-date-tied changes did not replicate the evolving CO<sub>2</sub> gas exchange of the forest properly in spring. Otherwise the models simulated the CO<sub>2</sub> exchange of the forest quite well.

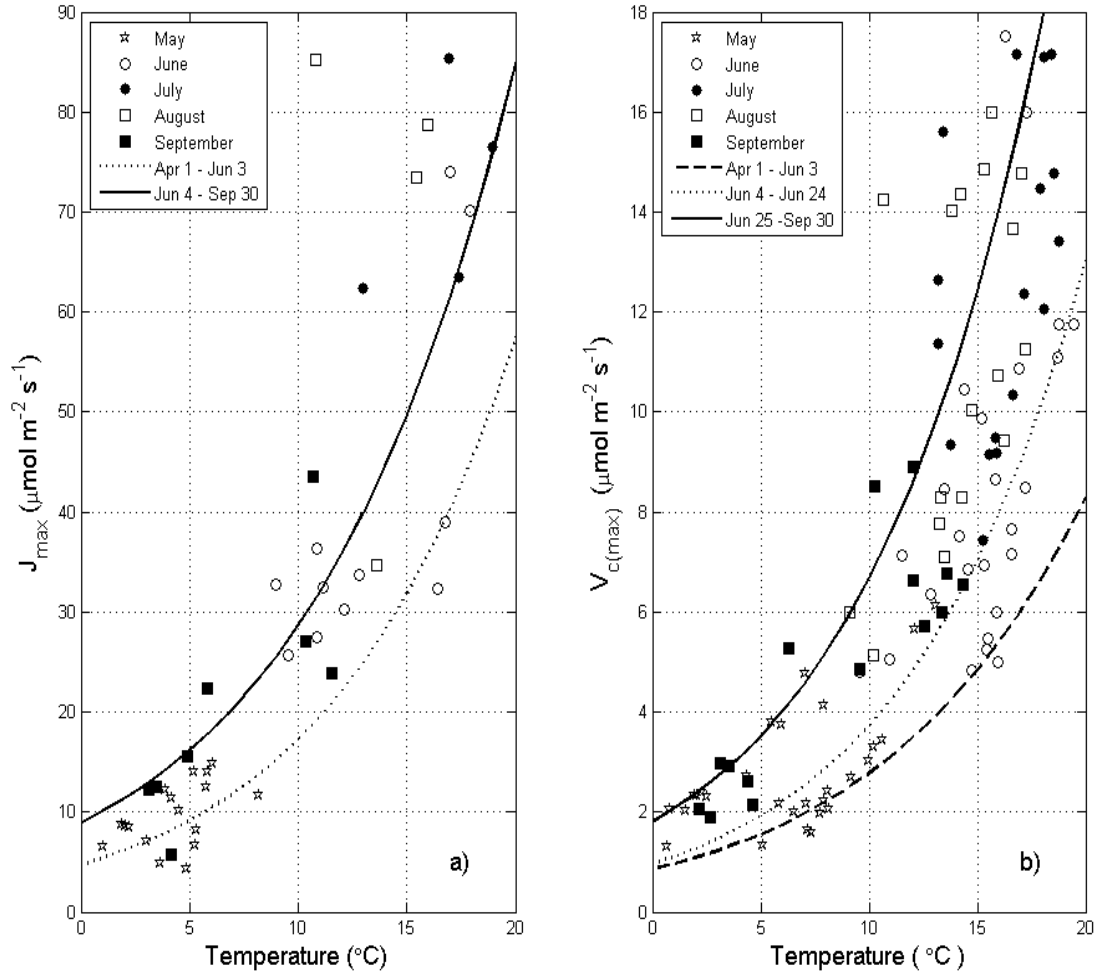


Figure 8. The temperature responses of parameters  $J_{max}$  (a) and  $V_{c(max)}$  (b) at Sodankylä. The points are inversed values from the half-hourly measurements, and the lines are exponential fits made for different time periods (**Paper II**).

The capacity of these models to simulate the dry period in June 2001 was studied. Neither of the models was able to replicate the effect of drought on the  $\text{CO}_2$  gas exchange. A new coefficient to replicate drought was introduced into the Ball-Berry stomatal conductance and this did improve the model performance, but to properly model the effect of drought a full soil model should be coupled to the canopy model.

### 4.3. Assessing seasonality through biochemical model parameters in a canopy-level model

The parameterization of the biochemical model at Sodankylä in a previous study (**Paper II**) revealed a seasonal pattern in the model parameters. This provided an incentive for studying the phenomenon more closely, so as to find out if it is characteristic of the boreal forest in general, and if so, whether it also occurs in more southern forests. Examining the parameters at different sites would reveal any quantitative differences between species and their latitudinal location. The difficulty of simulating the emergence of the CO<sub>2</sub> fluxes in differently evolving springs was also addressed in the previous study and methods to improve this were experimented with. The importance of the seasonally-varying temperature dependences was also an open question.

The parameterization of the biochemical model was performed for four sites (**Paper III**). In addition to the Sodankylä site introduced earlier, the sites included the spruce forest of Kenttäröva in Finnish Lapland, the Scots pine forest of Hyytiälä in central Finland and the southernmost site of Norunda, a mixed Scots pine/Norway spruce location in central Sweden (Table 1 and Fig. 5). The results were similar to Sodankylä. The parameter  $J_{max}$  had one temperature fit for Norunda, two at Kenttäröva and three at Hyytiälä. The parameter  $V_{c(max)}$  had two different temperature fits at Kenttäröva and Norunda, and four at Hyytiälä. At Hyytiälä the measurement time series was the most continuous of the sites, thus allowing for more fits than at other sites. Most of these temperature responses changed during spring-time, but at Hyytiälä an autumn-time fit for  $V_{c(max)}$  was also obtained. Apart from this, the magnitudes of the biochemical parameters in summer were similar at all the four sites.

To improve the modelling results, the dates when the temperature fits change to another, the so-called changeover dates, were bound to temperature indices. The temperature sum, i.e., the sum of positive daily average temperatures, and the five-day average temperature (5Dave) were chosen. They were used to mark the changeover date in the parameterization year and then this value was used to locate changeover dates in other years when the model was run. The simulated CO<sub>2</sub> fluxes were improved.

The sensitivity of the model to various variables was studied. The model is sensitive to leaf area on a daily scale, but not on an annual scale, and adding the seasonal development of leaf biomass did not cause major changes in the results. The seasonally-changing temperature dependences of the model parameters had a major effect on the annual GPP, compared to the use of a summertime fit only: the seasonally-changing fitting decreased GPP by 17%. The effect of late night-frosts in spring in lowering the parameter values was noticed, but this was not successfully replicated by modelling efforts. The lowering of the parameter values after night frosts most probably results from a reversal of the spring recovery, as described by Ensminger et al. (2004).

#### 4.4. Tracking seasonality with meteorological and biological variables

In previous work (**Paper III**), the changeover dates of different temperature fits were tied to temperature indices and improved modelling results were thus obtained. Temperature is one variable that can be used to assess the seasonal development of vegetation. Since it can be very useful in modelling, it was important to study how reliable it is and what other variables can be used similarly. The other variables that were studied included surface albedo, CO<sub>2</sub> concentration and chlorophyll fluorescence. The study sites were the same four sites as in the previous study. Because of the long-time series available, possible trends in spring recovery and autumn cessation were also looked for. The differences between the two northern and the two southern sites were also addressed (**Paper IV**).

The active period was defined according to Suni et al. (2003) as the time when the net CO<sub>2</sub> uptake of the forest exceeds 20% of the maximum summertime values (**Paper IV**). This time period is called the FGS (Flux Growing Season). This definition is directly connected to the CO<sub>2</sub> flux measurements, so it is also bound to the annual carbon balance.

The comparison between the thermal growing season and the growing season defined from EC measurements, the FGS, revealed FGS to have a considerably earlier onset and later ending than the thermal growing season at all of the four sites. The CO<sub>2</sub> flux measurements were used as a reference. Four different temperature-related indices represented earlier were studied: the five-day average temperature (5Dave), the state of acclimation (S), the temperature sum (TS) and the seasonal factor (f). The time constant used for S was 200 h (Kolari et al., 2007). One year of data was used to set the thresholds for the emergence and finishing of the CO<sub>2</sub> fluxes and then these thresholds were used to predict the active period for the other years. The temperature indices proved to be good proxies for FGS, 5Dave and S offering the best results. The most southern site of Norunda was challenging, since 5Dave and S did not work there properly, due to large fluctuations in their values over substantial time periods; in contrast, f and TS provided feasible estimations.

The start of the snow melt was a good estimate for the beginning of the FGS. It was assessed from ground-based and spaceborne surface albedo measurements. The chlorophyll fluorescence parameter  $F_v/F_m$  was also a good predictor for the start and end of the FGS. The CO<sub>2</sub> concentration data were used in two different methods, using the threshold method similarly to the other variables as well as a derivative method that enabled a larger-scale estimate. The threshold method gave predictions close to the two northern sites' FGS, while the derivative method gave predictions comparable with the FGS for Norunda. The differences between the various estimates for the beginning and end of the growing season and those of the FGS at Sodankylä are shown in Fig. 9 for several years. Estimates made using temperature-related indices, chlorophyll fluorescence, albedo and CO<sub>2</sub> concentration show quite good correspondence with the FGS dates.

Since the CO<sub>2</sub> concentration measurements extended to 1997, they were used to detect trends together with the temperature indices. A trend toward an earlier spring onset was found at Pallas/Sammaltunturi. A long time series of air temperature (1908-2005) was

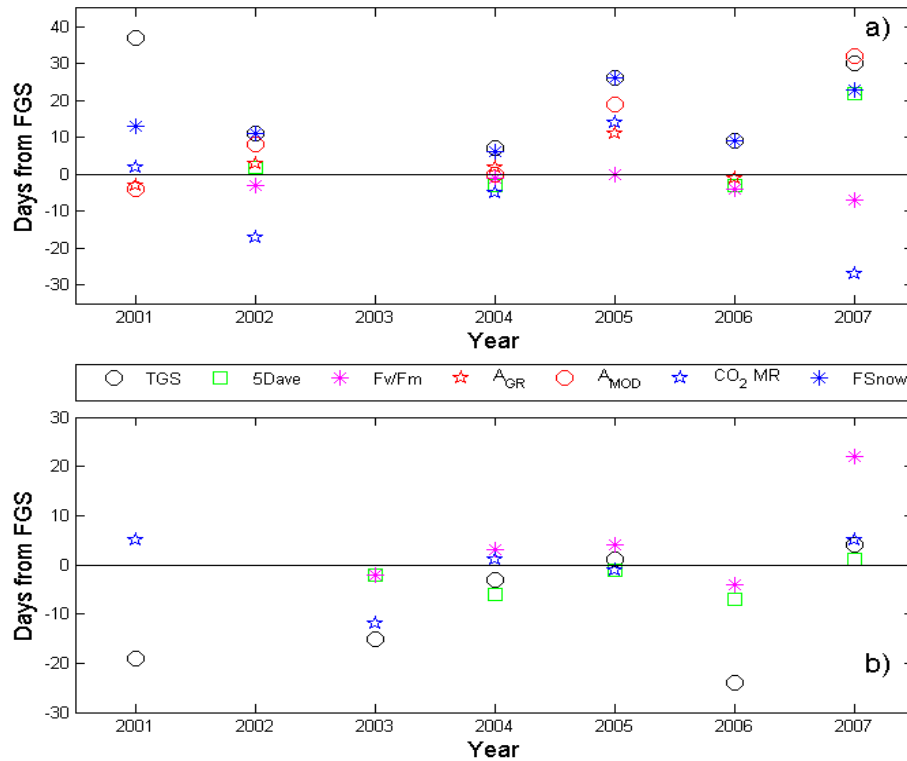


Figure 9. The difference between the start of the growing season (a) and the end of the growing season (b) at Sodankylä by different methods compared to FGS. FGS is the growing season defined from the CO<sub>2</sub> flux according to Suni et al. (2003). TGS is the thermal growing season, 5Dave is the five-day running average temperature, F<sub>v</sub>/F<sub>m</sub> is the chlorophyll fluorescence, A<sub>GR</sub> is the albedo measured at the ground level, A<sub>MOD</sub> is the albedo measured from the MODIS satellite and FSnow is the final day of the snow melt. CO<sub>2</sub> MR is a threshold defined from the five-day average CO<sub>2</sub> concentration at Pallas/Kenttäröva (**Paper IV**).

available for Sodankylä and Helsinki (60°11'N, 24°57'E), and when 5Dave was used to estimate the growing season length, a trend toward an earlier spring was also found at these two locations. When comparing northern and southern sites, it was noticed that in the south 5Dave and TS were lower in value than at the northern sites at the start of the growing season as defined by FGS.

Since the annual GPP was not assessed in this study (**Paper IV**), no conclusions can be drawn about whether an increase in the growing season will make boreal forests a stronger sink or a source. However, this work provides tools to assess this. It is most likely that the answer to this question is not simple. Arneeth et al. (2006) concluded that, in addition to the timing of the spring onset and the speed of snow melt, the climatic conditions during the rest of the year will also influence the carbon balance.

In addition to these analyses, a campaign to study the possibility of carrying out the passive detection of sun light-induced fluorescence was performed at Sodankylä in spring 2002 (**Paper V**). Measuring sun light-induced fluorescence with a passive detector was indeed feasible, and the course of the spring recovery could be tracked and linked with active measurements and the CO<sub>2</sub> flux measurements. However, the influence of the canopy structure during sunny days was strong, and some modelling would be needed in the interpretation of the results.

## 5. Discussion

In this study the photosynthesis parameters of the biochemical model have been assessed on many scales, starting from the chloroplastic level in the mesophyll cell all the way to the generalization of the parameters to a boreal coniferous forest. Some significant observations have been made that can be considered when further developing CO<sub>2</sub> gas exchange models.

The results from the three-dimensional leaf stomata model show that the physical transport processes influence the results of the parameters estimated by leaf-level gas exchange measurements. These effects might lead to biases in conclusions drawn from the measurement data. The differences in the parameter values between species might be partly structural, and the temperature responses at the microscopic level might vary. The insights obtained from the 3-D-model can be used when working with larger-scale models and the model can be used in parameterizing them. For example, it would be interesting to study differences in the microscopic structure along the latitudinal gradient and assess what kind of effect this structure has, i.e., what are the consequences for the biochemical parameters and their temperature responses. In addition, the effects of an enhanced CO<sub>2</sub> concentration in plants could be studied with this tool. Studying coniferous trees, e.g., Scots pine, would be interesting in order to see the effects caused by its different cellular structure.

When measuring at the leaf scale, the processes related to the cellular structure are lost, and only net amounts of CO<sub>2</sub> and H<sub>2</sub>O fluxes are obtained. The larger scale obscures the processes taking place at smaller scales. A similar thing happens when moving from the leaf-level to the canopy-level in a forest. There are ways of making quite good estimates of the green biomass of the forest, for example, but as in the earlier transition, some of the processes are ignored. These different processes can be modelled with our current physical knowledge, but the modelling assumptions will always be simplifications of reality.

In the canopy modelling part of this work, radiative transfer, shaded and sunlit leaves and the vertical gradient in the carboxylation efficiency were taken into account when upscaling the leaf-level photosynthesis models to the canopy level. All these processes have their limitations and, in addition, the use of eddy covariance data has its own challenges. Even though the eddy covariance method is currently widely used, there are some problems with the method that need to be considered when using the data. The first law of thermodynamics implies an energy balance closure, requiring that the sum of the estimated latent and sensible heat flux is equivalent to all other energy sinks and sources (Wilson et al., 2002). It has been

long known that the eddy covariance measurements have problems in closing this energy balance (Aubinet et al., 2000; Wilson et al., 2002) and thus do not follow the physical principle of conservation of energy. The inability to close the energy balance might be caused by advection or that part of the turbulence fluxes that the measurement is unable to capture, thus raising general questions about the reliability of the CO<sub>2</sub> flux measurements as well (Aubinet et al., 2000). The ability of the EC measurements to provide adequate data for the parameterization of land surface models has therefore been open to doubt, unless the energy fluxes involved are corrected to ensure the closure (El Maayar et al., 2008).

The problems of eddy covariance also include the difficulty of estimating night-time fluxes under stable conditions and the handling of a storage term that is the CO<sub>2</sub> gas accumulated on the forest floor during stable conditions (Aubinet et al., 2000). The eddy covariance data can be compared to other measurements. On short time-scales, the CO<sub>2</sub> fluxes by EC can be compared to chamber measurements (Lohila et al., 2007). On annual time scales, the net primary production estimated from EC measurements can be compared to biometric estimates (Curtis et al., 2002). In this work in modelling, only measurements in turbulent conditions were used (**Papers II-IV**) and no annual balances were assessed, so there was no need to analyse the measurement errors profoundly, even though they influence the estimated parameter values.

Despite their problems, EC data have been recommended for use in model parameterization (Hollinger and Richardson, 2005). EC data apply to canopy-scale parameters directly, thus avoiding the problem of upscaling the parameters estimated at the leaf level (Wang et al., 2006). Lately, EC data have been used in model-data fusion (MDF) to estimate the parameters needed in the models (Trudinger et al., 2007; Fox et al., 2009; Williams et al., 2009). MDF uses models and observations and takes into account their uncertainties, producing model parameterizations consistent with data as well as estimates of system dynamics with confidence intervals (Williams et al., 2005). Other estimation methods have also been used (Braswell et al., 2005; Wang et al., 2006). This work adopted a simpler approach, thus not obtaining error estimations for the parameters. However, taking the simple approach and concentrating on few sites only, enabled a more detailed insight into the forests and their dynamics.

The interpretation of inversed parameter values has two challenges, one being equifinality while the other relates to compensating mechanisms occurring because of model deficiencies or biases (Williams et al., 2009). Equifinality means different model parameters and structures yielding similar effects on model outputs that can be difficult to distinguish (Medlyn et al., 2005b). This can be an important issue in efforts to separate the effects of the light use efficiency factor  $q$  and  $J_{max}$  in the biochemical model (**Paper III**).

The inversed values for the biochemical parameters differ from the estimates at the leaf scale, the parameter  $J_{max}$  being higher. The leaf-scale estimate is a different parameter, the canopy-level parameter indicating a more integrated value, but in some inversion studies the parameter  $V_{c(max)}$  has been matched at these two scales (Santaren et al., 2007). Also the ratio between  $J_{max}$  and  $V_{c(max)}$  varies between seasons, even though, in the literature, this ratio is often considered to be constant. These deviations from the literature might indicate that

some essential processes are not being taken into account in the upscaling of the model. In addition, several error sources are present, e.g., in the estimation of respiration and changes in the vertical carboxylation efficiency, as well as measurement errors. The radiative transfer model that we used is widely used in modelling (Knorr and Heimann, 2001a), but it does not include some important characteristics of coniferous forests, such as clumping (Stenberg et al., 2001; Smolander and Stenberg, 2003). It would be important to also study the parameter estimation results with another radiative transfer model. For example, a canopy model has been developed for Finnish forests that takes into account the special features of a coniferous forest (Oker-Blom et al., 1989). The similar values obtained for the biochemical parameters in summer for the four boreal forest sites suggest that the parameters are generic in regional models and the PFT approach.

A seasonal pattern in the biochemical model parameters was revealed when the inversed parameter values were studied. This is most likely to be caused by some kind of seasonal adaptation of the plants. The biochemical model parameters have been found to vary seasonally in measurements (Wang, 1996; Xu and Baldocchi, 2003), but it has been suggested that the parameters in a process-based model should be constant, i.e., the driving variables should be the only ones that vary, while the modelled processes contain all other changes. The rate of photosynthesis is constrained by the leaf Rubisco nitrogen content and its activity status (Ainsworth and Long, 2005); in the biochemical model this is described by  $V_{c(max)}$ . Yuan et al. (2008) studied the carbon-cycle at seven Canadian forest sites, four of which were boreal and three temperate, using a carbon-cycle model that also included the nitrogen cycle. The photosynthesis parameters and their temperature relations proved to be important in the modelling, and using seasonally-changing  $V_{c(max)}$  and  $J_{max}$  improved results compared to earlier modelling studies with a prescribed  $V_{c(max)}$ . In their study they linked modelled leaf Rubisco-nitrogen and canopy temperature to calculate  $V_{c(max)}$  dynamically. Even though the Rubisco-nitrogen played a role in the seasonal dynamics of  $V_{c(max)}$ , the temperature was more influential. However, the site-specific values of leaf Rubisco-nitrogen varied more between different sites than they did seasonally. The seasonal variation in  $V_{c(max)}$  was more pronounced at boreal sites than at temperate sites (Yuan et al., 2008). This is in accordance with our results from Norunda, where the seasonal variation in the model parameters was not as noticeable as at the more northern sites. Also, the importance of the canopy temperature in the seasonal dynamics might indicate that we can use our model to study the controls of CO<sub>2</sub> gas exchange in a boreal forest without including the effects of nitrogen. Our model parameters are not estimated in relation to canopy temperature but air temperature. The use of canopy temperature in the parameterizations was examined at Sodankylä, but since it did not have any significant effect on the results, air temperature was used.

Conductance was also important in the model study in Canada (Yuan et al., 2008). There are implications that conductance could also have seasonal dynamics (Medlyn et al., 2002a). A seasonally-varying conductance might also influence the  $V_{c(max)}$  and  $J_{max}$  values. This has been studied preliminarily at Sodankylä (Thum et al., 2009). Conductance did indeed show a seasonal behaviour, but its effect was not seen in the inversed  $V_{c(max)}$  and  $J_{max}$  values.



In contrast to the results presented here, Williams et al. (2009) state as their opinion that the model parameters should remain constant in time and that changing parameters would be an indication of missing process representation. They presented a case from the ORCHIDEE biogeochemical model in which annually-estimated  $V_{c(max)}$  by data assimilation was changing at two sites out of four, and concluded that some processes are missing, probably those related to the nitrogen cycle. The study by Yuan et al. (2008) contradicts this conclusion by also bringing up the importance of temperature. It is likely that the biochemical model parameters' variation can be explained by additional processes, but the present work only presents the importance of these variations and simple methods of tackling the problem. Adding information about the photochemical state of the plant, by using chlorophyll fluorescence or frost hardiness (Leinonen et al., 1997), might be ways of overcoming this. Temperature-acclimated biochemical model parameters have been used successfully in recent canopy-level CO<sub>2</sub> gas exchange modelling (Verbeeck et al., 2008; Delpierre et al., 2009).

Williams et al. (2009) also argue that estimating only some parameters, instead of estimating them all, may not include key processes and is therefore equivalent to keeping those other parameters constant. Estimation of all the parameters lies beyond the scope of this work, and only some sensitivity analysis was performed in this respect (**Paper III**). Even though all the parameters are approximated using the Bayesian approach, obviously only processes described in the model are included. The Bayesian method is also known to be very sensitive to the uncertainty limits provided before calculation (Knorr and Kattge, 2005) and even though all the parameters are treated equally and simultaneously, only some can, in the end, be constrained by the eddy covariance data (Knorr and Kattge, 2005). This method might include some pitfalls when applied to sites with unusual parameter values. The models in general can be used to simulate, e.g., carbon balances or they can be used to test and improve our knowledge of different processes. The models should only be criticized in respect to their objectives (Thornley and Johnson, 1990). The Bayesian approach is numerically sound and provides error estimates. However, the approach used in this work allows insights into which processes are missing from the model formulation.

The optimal stomatal (OM) model proved to be useful at Sodankylä (**Paper II**) as a canopy level model to be used, e.g., in gap-filling but it does not have characteristics of a model to be used in future scenario simulations. Some overestimation at high light levels was noticed in the modelling results, but this effect could possibly be corrected by tuning the parameters. Tuning the parameters however raises questions about the applicability of the model, since the parameters were obtained from Värriö, a Scots pine site located in Finnish Lapland at the same latitude as Sodankylä. The parameters of the OM model were studied in more detail by Kolari et al. (2007) at shoot level at both the Hyytiälä and Värriö sites, and some differences between the model parameters obtained ( $\lambda$  and  $\gamma$ ) were found. This indicates that the biochemical model parameters could be more generalized than the OM model parameters when comparing the results of Kolari et al. (2007) with the results from **Paper III**. However, the overall results by the OM model at Sodankylä were good and at a satisfactory level for a canopy model. These simple models can be useful in obtaining estimates for annual carbon balances and in the gap-filling of discontinuous eddy covariance measurements. In addition, they are simple to parameterize and thus very useful (Verbeeck

et al., 2008). However, since the OM model does not contain responses to an increasing CO<sub>2</sub> concentration, it is not suitable for use in scenario runs for the future climate.

The climate models still need some improvements when it comes to estimation of the seasonal cycle of plant growth (Sasai et al., 2007; Ricciuto et al., 2008). In addition, the forest carbon simulation model has recently been improved by replacing the old temperature-sum-based estimate by one with the addition of a chilling factor (Chiang and Brown, 2007). Tanja et al. (2003) introduced a way to of linking the five-day average temperature (5Dave) to CO<sub>2</sub> flux measurements. In **Paper IV** this approach was taken one step further by correlating the CO<sub>2</sub> fluxes with some meteorological and biological variables. The changes in the atmospheric CO<sub>2</sub> concentration are created by the CO<sub>2</sub> gas exchange between the atmosphere and vegetation, whereas surface albedo and temperature are purely meteorological variables. Rising temperatures in spring are drivers for the recovery of photosynthetic activity, but during the autumn the photoperiod also plays a role in the diminishing of the CO<sub>2</sub> gas exchange. In **Paper IV** the temperature-related indices were, however, successful in predicting both the start and the end of the FGS. The CO<sub>2</sub> concentration was useful in this context as well, but it is a larger-scale measurement. Surface albedo can be used in estimating the onset of CO<sub>2</sub> exchange in the spring (Kimball et al., 2004), as it reveals when the surface water becomes available to plants (Jarvis and Linder, 2000).

Chlorophyll fluorescence was a reliable proxy for the growing season (**Paper IV**), except for one autumn at Sodankylä. The photosynthetic capacity remained high in warm conditions even though the light conditions led to a diminishing of photosynthesis. Thus when the chlorophyll fluorescence parameters are used in estimation of the growing season, the environmental conditions also need to be taken into account. Chlorophyll fluorescence is of great applicability, since substantial progress towards its remote sensing has been made during the last few years (Meroni et al., 2009).

## 6. Conclusions

This study focused on the role of temperature as a determinant of carbon fluxes in boreal coniferous forests, with a special emphasis on scaling up from leaf-level eco-physiological processes to the whole canopy. The stomata-level CO<sub>2</sub> gas exchange of a birch leaf was assessed with a detailed 3-D model (**Paper I**). This revealed the role of the physical processes taking part in the process and their importance when interpreting the results from leaf chamber measurements. This method can be further used in parameterization of mesophyll conductance to larger-scale models.

Using eddy covariance data for parameterizing two upscaled CO<sub>2</sub> gas exchange models showed the role of seasonality in the parameters of the biochemical model, and that temperature is a suitable driving variable to describe the seasonality in the OM model (**Paper II**). The seasonality of the biochemical model parameters was assessed in a later

study at different sites, and similar seasonal behaviour was found (**Paper III**). The taking into account of this seasonal behaviour in modelling was found to be important. A method of linking temporally-changing biochemical parameter values to temperature indices was also developed in this study. In later work these temperature indices, together with other environmental and biological variables, were connected to canopy CO<sub>2</sub> gas exchange measurements (**Paper IV**). The results of the applicability of these variables to predict the active season of vegetation were assessed and found to be good; two of them were used to calculate trends. Five-day average temperatures exhibited a trend towards an earlier spring onset in both southern and northern Finland over a 98-year time period, and a trend towards an earlier spring was also found using an 11-year long measurement series of CO<sub>2</sub> concentrations at Pallas/Sammaltunturi.

It is essential that the characteristics of boreal forests are studied in detail. This enables further model parameterization to be used in larger-scale models. The results of this work can be used in model development. Linking environmental variables directly to CO<sub>2</sub> fluxes is useful in studying trends and is an important step in assimilating data into models. The effect that temporally-changing biochemical model parameters had on annual GPP was significant, and brings out the importance of further studying these issues. This might also improve the phenomenology description of the boreal forests in the larger-scale models used currently. The use of eddy covariance data in a simple upscaled model enables the study of ecosystem functioning at a very high temporal resolution compared to leaf chamber measurements. This can provide us with a deeper insight into the controls underlying the CO<sub>2</sub> gas exchange of vegetation.

Connections between meteorological and biological variables and CO<sub>2</sub> gas exchange should also be established in more temperate ecosystems in order to see whether the results of this work are similar, or are only applicable in boreal forests. Adding evapotranspiration to the model enables the use of afternoon measurements, thus increasing the amount of usable data and making the study of the conductance parameters and their seasonal behaviour also feasible. Studies using chlorophyll fluorescence measurements might enable a separation of the changes in the frost hardiness and photochemical efficiency during the transition periods between winter and summer.

Generalizing the results of this work would make a substantial improvement in the modelling of the northern forest CO<sub>2</sub> exchange. It would be interesting to see how implementing the results of this work in larger-scale models would influence their results.

## References

- Aalto, T., 1998. Carbon dioxide exchange of Scots pine shoots as estimated by a biochemical model and cuvette field measurements. *Silva Fennica* 32, 321-337.
- Aalto, T., Hatakka, J., Paatero, J., Tuovinen, J.-P., Aurela, M., Laurila, T., Holmén, K., Trivett, N., and Viisanen, Y., 2002. Tropospheric carbon dioxide concentrations at a northern boreal site in Finland: basic variations and source areas. *Tellus* 54B, 110-126.
- Aalto, T., and Juurola, E., 2001. Parametrization of a biochemical CO<sub>2</sub> exchange model of birch

- (*Betula pendula* Roth.). *Boreal Environment Research* 6, 53-64.
- Aalto, T., and Juurola, E., 2002. A three-dimensional model of CO<sub>2</sub> transport in airspaces and mesophyll cells of a silver birch leaf. *Plant, Cell and Environment* 25, 1399-1409.
- Ainsworth, E. A., and Long, S. P., 2005. What have we learned from 15 years of free-air CO<sub>2</sub> enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>. *New Phytologist* 165, 351-372.
- Andersson, I., 2008. Catalysis and regulation in Rubisco. *Journal of Experimental Botany* 59, 1555-1568.
- Arneeth, A., Lloyd, J., Shibistova, O., Sogachev, A., and Kolle, O., 2006. Spring in the boreal environment: observations on pre- and post-melt energy and CO<sub>2</sub> fluxes in two central Siberian ecosystems. *Boreal Environment Research* 11, 311-328.
- Aubinet, M., Grelle, A., Ibrom, A., Rannik, Ü., Moncrieff, J., Foken, T., Kowalski, A. S., Matrin, P. H., Berbigier, P., Bernhofer, Ch., Clement, R., Elbers, J., Granier, A., Grünwald, T., Morgenstern, K., Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., and Vesala, T., 2000. Estimates of the annual net carbon and water exchange of forests: The EUROFLUX methodology. *Advances in Ecological Research* 30, 113-175.
- Aurela, M., 2005. Carbon dioxide exchange in subarctic ecosystems measured by a micrometeorological technique. *Contributions* 51, Finnish Meteorological Institute, Helsinki, Finland, 132 pp.
- Baker, N. R., 2008. Chlorophyll fluorescence: A probe of photosynthesis in vivo. *Annual Review of Plant Biology* 59, 89-113.
- Baldocchi, D., 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biology* 9, 479-492.
- Ball, J. T., Woodrow, I. E., and Berry, J. A., 1987. A model for predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: *Progress in photosynthesis research* (ed. I. Biggins), Vol IV. Martinus Nijhoff Publishers, Netherlands, 221-224.
- Bartsch, A., Kidd, R. A., Wagner, W., and Bartalis, Z., 2007. Temporal and spatial variability of the beginning and end of daily spring freeze/thaw cycles derived from scatterometer data. *Remote Sensing of Environment* 106, 360-374.
- Berry, J., and Björkman, O., 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* 31, 491-543.
- Bonan, G. B., 2008a. *Ecological Climatology*. Cambridge University Press, New York. 550 pp.
- Bonan, G. B., 2008b. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320, 1444-1449.
- Bonan, G. B., Chapin III, F. S., and Thompson, S. L., 1995. Boreal forest and tundra ecosystems as components of the climate system. *Climatic Change* 29, 145-167.
- Braswell, B. H., Sacks, W. J., Linder, E., and Schimel, D. S., 2005. Estimating diurnal to annual ecosystem parameters by synthesis of a carbon flux model with eddy covariance net ecosystem exchange observations. *Global Change Biology* 11, 335-355.
- Bronson, D. R., Gower, S. T., Tanner, M., and Van Herk, I., 2009. Effect of ecosystem warming on boreal black spruce bud burst and shoot growth. *Global Change Biology* 15, 1534-1543.
- Brooks, A., and Farquhar, G. D., 1985. 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.
- Campbell, N. A., and Reece, J. B., 2005. *Biology*. Benjamin and Cummings, San Francisco, The United States, 1231 pp.
- Canadell, J. G., Le Quéré, C., Raupach, M. R., Field, C. B., Buitenhuis, E. T., Ciais, P., Conway, T. J., Gillett, N. P., Houghton, R. A., and Marland, G., 2007. Contributions to accelerating atmospheric CO<sub>2</sub> growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Science* 104, 18866-18870.

- Chiang, J.-M., and Brown, K. J., 2007. Improving the budburst phenology subroutine in the forest carbon model PnET. *Ecological Modelling* 205, 515-526.
- Churkina, G., Schimel, D., Braswell, B. H., and Xiao, X., 2005. Spatial analysis of growing season length control over net ecosystem exchange. *Global Change Biology* 11, 1777-1787.
- Ciais, P., Peylin, P., and Bousquet, P., 2000. Regional biospheric carbon fluxes as inferred from atmospheric CO<sub>2</sub> measurements. *Ecological Applications* 10, 1574-1589.
- Cowan, I.R., 1977. Stomatal behavior and the environment. *Advances of Botanical Research* 4, 117-227.
- Curtis, P. S., Hanson, P. J., Bolstad, P., Barford, C., Randolph, J. C., Schmid, H. P., and Wilson, K. B., 2002. Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agricultural and Forest Meteorology* 113, 3-19.
- Dang, Q.-L., Margolis, H. A., and Collatz, G. J., 1998. Parameterization and testing of a coupled photosynthesis-stomatal conductance model for boreal trees. *Tree Physiology* 18, 141-153.
- Davidson, E. A., and Janssens, I., 2006. Temperature sensitivity of soil carbon decomposition and feedback to climate change. *Nature* 440, 165-173.
- De Pury, D. G. G., and Farquhar, G. D., 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant, Cell and Environment* 20, 539-557.
- Delpierre, N., Soudani, K., François, C., Köstner, B., Pontailler, J.-Y., Nikinmaa, E., Misson, L., Aubinet, M., Bernhofer, C., Granier, A., Grünwald, T., Heinesch, B., Longdoz, B., Ourcival, J.-M., Rambal, S., Vesala, T., and Dufrêne, E., 2009. Exceptional carbon uptake in European forests during the warm spring of 2007: a data-model analysis. *Global Change Biology* 15, 1455-1474.
- Denning, S., Nicholls, M., Prihodko, L., Baker, I., Vidale, P.-L., Davis, K., and Bakwin, P., 2003. Simulated variations in atmospheric CO<sub>2</sub> over a Wisconsin forest using a coupled ecosystem-atmosphere model. *Global Change Biology* 9, 1241-1250.
- Dong, J., Kaufmann, R. K., Myneni, R. B., Tucker, C. J., Kauppi, P. E., Liski, J., Buermann, W., Alexeyev, V., and Hughes, M. K., 2003. Remote sensing estimates of boreal and temperate forest woody biomass: carbon pools, sources, and sinks. *Remote Sensing of Environment* 84, 393-410.
- Dunn, A. L., Barford, C. C., Wofsy, S. C., Goulden, M. L., and Daube, B. C., 2007. A long-term record of carbon exchange on a boreal black spruce forest: means, responses to interannual variability and decadal trends. *Global Change Biology* 13, 577-590.
- El Maayar, M., Chen, J. M., and Price, D. T., 2008. On the use of field measurements of energy fluxes to evaluate land surface models. *Ecological Modelling* 214, 293-304.
- Ensminger, I., Busch, F., and Huner, N. P. A., 2006. Photostasis and cold acclimation: sensing low temperatures through photosynthesis. *Physiologia Plantarum* 126, 28-44.
- Ensminger, I., Sveshnikov, D., Campbell, D. A., Funk, C., Jansson, S., Lloyd, J., Shibistova, O., and Öquist, G., 2004. Intermittent low temperatures constrain spring recovery of photosynthesis in boreal Scots pine forests. *Global Change Biology* 10, 995-1008.
- Ensminger, I., Schmidt, L., and Lloyd, J., 2008. Soil temperature and intermittent frost modulate the rate of recovery of photosynthesis in Scots pine under simulated spring conditions. *New Phytologist* 177, 428-442.
- Farquhar, G. D., von Caemmerer, S., and Berry, J.A., 1980. A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta* 149, 78-90.
- Farquhar, G. D., and von Caemmerer, S., 1982. Modelling of photosynthetic response to environmental conditions. In: Lange, O. L., Nobel, P. S., Osmond, C. B., and Ziegler, H. (eds.), *Encyclopedia of Plant Physiology* 12B, 550-587. Springer-Verlag, Berlin, Germany.
- Finnigan, J., Clement, R., Malhi, Y., Leuning, R., and Cleugh, H. A., 2003. A re-evaluation of long-term flux measurement techniques, Part I: Averaging and coordinate rotation. *Boundary-Layer Meteorology* 107, 1-48.
- Finnish Meteorological Institute 1991. Climatological Statistics in Finland 1961-1990, *Supplement*

- to the *Meteorological Yearbook of Finland*, The Finnish Meteorological Institute, Helsinki, Finland.
- Foley, J. A., Costa, M. H., Delire, C., Ramankutty, N., and Snyder, P., 2003. Green surprise? How terrestrial ecosystems could affect earth's climate. *Frontiers in Ecology and the Environment* 1, 38-44.
- Fox, A., Williams, A., Richardson, A. D., Cameron, D., Gove, J. H., Quaife, T., Ricciuto, D., Reichstein, M., Tomelleri, E., Trudinger, C., and Van Wijk, M. T., 2009. The REFLEX project: Comparing different algorithms and implementations for the inversion of a terrestrial ecosystem model against eddy covariance data. *Agricultural and Forest Meteorology* 149, 1597-1615.
- Foyer, C. H., Bloom, A. J., Queval, G., and Noctor, G., 2009. Photorespiratory metabolism: genes, mutants, energetics, and redox signaling. *Annual Review of Plant Biology* 60, 455-484.
- Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H. D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K.-G., Schnur, R., Strassmann, K., Weaver, A. J., Yoshikawa, C., and Zeng, N., 2006. Climate-carbon cycle feedback analysis: Results from the C<sup>4</sup>MIP model intercomparison. *Journal of Climate* 19, 3337-3353.
- Goodale, C. I., Apps, M. J., Birdsey, R. A., Field, C. B., Heath, L. S., Houghton, R. A., Jenkins, J. C., Kohlmaier, G. H., Kurz, W., Liu, S., Nabuurs, G.-J., Nilsson, S., and Shvidenko, A. Z., 2002. Forest carbon sinks in the northern hemisphere. *Ecological Applications* 12, 891-899.
- Gower, S. T., Krankina, O., Olson, R. J., Apps, M., Linder, S., and Wang, C., 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. *Ecological Applications* 11, 1395-1411.
- Grelle, A., Lindroth, A., and Mölder, M., 1999. Seasonal variation of boreal forest surface conductance and evaporation. *Agricultural and Forest Meteorology*. 98-99, 563-578.
- Gurevitch, J., Scheiner, S. M., and Fox, G. A., 2002. *The ecology of plants*. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts, USA, 523 pp.
- Hari, P., and Kulmala, L. (eds.), 2009. *Boreal forest and climate change*. Springer. 582 pp.
- Hari, P., and Luukkanen, O., 1974. Field studies of photosynthesis as affected by water stress, temperature, and light in birch. *Physiologia Plantarum* 32, 97-102.
- Hari, P., and Mäkelä, A., 2003. Annual pattern of photosynthesis in Scots pine in the boreal zone. *Tree Physiology* 23, 145-155.
- Hari, P., Mäkelä, A., Berninger, F., and Pohja, T., 1999. Field evidence for the optimality hypothesis of gas exchange in plants. *Australian Journal of Plant Physiology* 26, 239-244.
- Hari, P., Mäkelä, A., Korpilähti, E., and Holmberg, M., 1986. Optimal control of gas exchange. *Tree Physiology* 2, 169-175.
- Hari, P., Mäkelä, A., and Pohja, T., 2000. Surprising implications of the optimality hypothesis of stomatal regulation gain support in a field test. *Australian Journal of Plant Physiology* 27, 77-80.
- Harley, P. C., and Baldocchi, D., 1995. Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. I. Leaf model parametrization. *Plant, Cell and Environment* 18, 1146-1156.
- Hatakka, J., Aalto, T., Aaltonen, V., Aurela, M., Hakola, H., Komppula, M., Laurila, T., Lihavainen, H., Paatero, J., Salminen, K., and Viisanen, Y., 2003. Overview of atmospheric research activities and results at Pallas GAW station. *Boreal Environment Research* 8, 365-384.
- Hollinger, D. Y., Kelliher, F. M., Schulze E.-D., Bauer, G., Arneth, A., Byers, J. N., Hunt, J. E., McSeveny, T. M., Kobak, K. I., Milukova, I., Sogatchev, A., Tatarinov, F., Varlargin, A., Ziegler, W., and Vygodskaya, N. N., 1998. Forest-atmosphere carbon dioxide exchange in eastern Siberia. *Agricultural and Forest Meteorology* 90, 291-306.
- Hollinger, D. Y., and Richardson, A. D., 2005. Uncertainty in eddy covariance measurements and its

- application to physiological models. *Tree Physiology* 25, 873-885.
- IPCC, 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Solomon S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. R. (eds.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 996 pp.
- Jarvis, P., and Linder, S., 2000. Constraints to growth of boreal forests. *Nature* 405, 904-905.
- Karlsen, S. R., Solheim, I., Beck, P. S. A., Hogda, K. A., Wielgolaski, F. E., and Tommervik, H., 2007. Variability of the start of the growing season in Fennoscandia, 1982-2002. *International Journal of Biometeorology* 51, 513-524.
- Kattge, J., and Knorr, W., 2007. Temperature acclimation in a biochemical model of photosynthesis: A reanalysis of data from 36 species. *Plant, Cell and Environment* 30, 1176-1190.
- Kattge, J., Knorr, W., Raddatz, T., and Wirth, C., 2009. Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology* 15, 976-991.
- Kellomäki, S., and Wang, K.-Y., 2000. Short-term environmental controls on carbon dioxide flux in a boreal coniferous forest: model computation compared with measurements by eddy covariance. *Ecological Modelling* 128, 63-88.
- Kimball, J. S., McDonald, K. C., Running, S. W., and Frolking, S. E., 2004. Satellite radar remote sensing of seasonal growing seasons for boreal and subalpine evergreen forests. *Remote Sensing of Environment* 90, 243-258.
- Knorr, W., and Heimann, M., 2001a. Uncertainties in global terrestrial biosphere modelling, Part I: A comprehensive sensitivity analysis with a new photosynthesis and energy balance scheme. *Global Biogeochemical Cycles* 15, 207-225.
- Knorr, W., and Heimann, M., 2001b. Uncertainties in global terrestrial biosphere modelling, Part II: Global constraints for a process-based vegetation model. *Global Biogeochemical Cycles* 15, 227-246.
- Knorr, W., and Kattge, J., 2005. Inversion of terrestrial ecosystem model parameter values against eddy covariance measurements by Monte Carlo sampling. *Global Change Biology* 11, 1333-1351.
- Kolari, P., Lappalainen, H. K., Hänninen, H., and Hari, P., 2007. Relationship between temperature and the seasonal course of photosynthesis in Scots pine at northern timberline and in southern boreal zone. *Tellus* 59B, 542-552.
- Kosugi, Y., and Matsuo, N., 2006. Seasonal fluctuations and temperature dependence of leaf gas exchange parameters of co-occurring evergreen and deciduous trees in a temperate broad-leaved forest. *Tree Physiology* 26, 1173-1184.
- Kozlowski, T. T., and Pallardy, S. P., 1997. *Physiology of woody plants*. Second edition. Academic Press, San Diego, California, USA. 411 pp.
- Kull, O., and Jarvis, P.G., 1995. The role of nitrogen in a simple scheme to scale up photosynthesis from leaf to canopy. *Plant, Cell and Environment* 18, 1174-1182.
- Kuzyakov, Y., and Cheng, W., 2001. Photosynthesis controls of rhizosphere respiration and organic matter decomposition. *Soil Biology & Biochemistry* 33, 1915-1925.
- Lagergren, F., Eklundh, L., Grelle, A., Lundblad, M., Mölder, M., Lankreijer, H., and Lindroth, A., 2005. Net primary production and light use efficiency in a mixed coniferous forest in Sweden. *Plant, Cell and Environment* 28, 412-423.
- Lagergren, F., Lindroth, A., Dellwik, E., Ibrom, A., Lankreijer, H., Launiainen, S., Mölder, M., Kolari, P., Pilegaard, K., and Vesala, T., 2008. Biophysical controls on CO<sub>2</sub> fluxes of three northern forests based on long-term eddy covariance data. *Tellus* 60B, 143-152.
- Laisk, A., and Loreto, F., 1996. Determining photosynthetic parameters from leaf CO<sub>2</sub> exchange and chlorophyll fluorescence. *Plant Physiology* 110, 903-912.
- Lawlor, D. W., 1993. *Photosynthesis: Molecular, Physiological and Environmental Processes*.

- Longman Scientific & Technical, Essex, England, 318 pp.
- Leinonen, I., Repo, T., and Hänninen, H., 1997. Changing environmental effects on frost hardiness of Scots pine during dehardening. *Annals of Botany-London* 79, 133-137.
- Lenton, T. M., Held, H., Kriegler, E., Hall, J. W., Lucht, W., Rahmstorf, S., and Schellnhuber, H. J., 2008. Tipping elements in the Earth's climate system. *Proceedings of the National Academy of Science* 105, 1768-1793.
- Leuning, R., 2002. Temperature dependence of two parameters in a photosynthesis model. *Plant, Cell and Environment* 25, 1205-1210.
- Lloyd, J., Shibistova, O., Zolotoukhine, D., Kolle, O., Arneth, A., Wirth, C., Styles, J. M., Tchebakova, N. M., and Schulze, E.-D., 2002. Seasonal and annual variations in the photosynthetic productivity and carbon balance of a central Siberian pine forest. *Tellus* 54B, 590-610.
- Lloyd, J., Syvertsen, J. P., Kriedemann, P. E., and Farquhar, G. D., 1992. Low conductances for CO<sub>2</sub> diffusion from stomatal to the sites of carboxylation in leaves of woody species. *Plant, Cell and Environment* 15, 873-899.
- Lloyd, J. and Taylor, J. A., 1994. On the temperature dependence of soil respiration. *Functional Ecology* 8, 315-323.
- Lohila, A., 2008. Carbon dioxide exchange on cultivated and afforested boreal peatlands. *Finnish Meteorological Institute Contributions* 73, Helsinki, Finland, 110 pp.
- Lohila, A., Aurela, M., Regina, K., Tuovinen, J.-P., and Laurila, T., 2007. Wintertime CO<sub>2</sub> exchange in a boreal agricultural peat soil. *Tellus* 59B, 860-874.
- Lundmark, T., Bergh, J., Strand, M., and Koppel., A., 1998. Seasonal variation of maximum photochemical efficiency in boreal Norway spruce stand. *Trees* 13, 63-67.
- Mäkelä, A., 2003. Process-based modelling of tree and stand growth: towards a hierarchical treatment of multiscale processes. *Canadian Journal of Forest research* 33, 398-409.
- Mäkelä, A., Berninger, F., and Hari, P., 1996. Optimal control of gas exchange during drought: theoretical analysis. *Annals of Botany* 77, 461-467.
- Mäkelä, A., Hari, P., Berninger, F., Hänninen, H., and Nikinmaa, E., 2004. Acclimation of photosynthetic capacity in Scots pine to the annual cycle of temperature. *Tree Physiology* 24, 369-376.
- Mäkelä, A., Kolari, P., Karimäki, J., Nikinmaa, E., Perämäki, M. and Hari, P., 2006. Modelling five years of weather-driven variation of GPP in a boreal forest. *Agricultural and Forest Meteorology* 139, 382-398.
- Markkanen, T., Rannik, Ü., Keronen, P., Suni, T., and Vesala, T., 2001. Eddy covariance fluxes over a boreal Scots pine forest. *Boreal Environment Research* 6, 65-78.
- Markkanen, T., Rannik, Ü., Marcolla, B., Cescatti, A., and Vesala, T., 2003. Footprints and fetches for fluxes over forest canopies with varying structure and density. *Boundary-Layer Meteorology* 106, 437-459.
- Matthews, H. D., Eby, M., Ewen, T., Friedlingstein, P., and Hawkins, B. J., 2007. What determines the magnitude of carbon cycle-climate feedbacks? *Global Biogeochemical Cycles* 21, GB2012, doi:10.1029/2006GB002733.
- Maxwell, K., and Johnson, G. N., 2000. Chlorophyll fluorescence – a practical guide. *Journal of Experimental Botany* 61, 659-668.
- Medlyn, B. E., Badeck, F.-W, de Pury, D. G. G., Barton, C. V., Broadmeadow, M., Ceulemans, R., de Angelis, P., Forstreuter, M., Jach, M. E., Kellomäki, S., Laitat, E., Marek, M., Philippot, S., Rey, A., Strassemeier, J., Laitinen, K., Liozon, R., Portier, B., Roberntz, P., Wang, K., and Jarvis, P.G., 1999. Effects of elevated [CO<sub>2</sub>] on photosynthesis in European forest species: a meta-analysis of model parameters. *Plant, Cell and Environment* 22, 1475-1495.
- Medlyn, B. E., Dreyer, E., Ellsworth, D., Forstreuter, M., Harley, P. C., Kirschbaum, M. U. F., Le Roux, X., Montpied, P., Strassemeier, J., Walcroft, A., Wang, K., and Loustau, D., 2002a. Temperature response of parameters of a biochemically based model of photosynthesis. II. A



- review of experimental data. *Plant, Cell and Environment* 25, 1167-1179.
- Medlyn, B. E., Loustau, D., and Delzon, S., 2002b. Temperature response of parameters of a biochemically based model of photosynthesis. I. Seasonal changes in mature maritime pine (*Pinus Pinaster* Ait.). *Plant, Cell and Environment* 25, 1155-1165.
- 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., 2005a. Carbon balance of coniferous forests growing in contrasting climates: Model-based analysis. *Agricultural and Forest Meteorology* 131, 97-124.
- Medlyn, B. E., Robinson, A. P., Clement, R., and McMurtrie, R. E., 2005b. On the validation of models of forest CO<sub>2</sub> exchange using eddy covariance data: some perils and pitfalls. *Global Change Biology* 25, 839-857.
- Meroni, M., Rossini, M., Guanter, L., Alonso, L., Rascher, U., Colombo, R., and Moreno, J., 2009. Remote sensing of solar-induced chlorophyll fluorescence: Review of methods and applications. *Remote Sensing of Environment* 113, 2037-2051.
- Moncrieff, J., Clement, R., Finnigan, J., and Meyers, T., 2004. Averaging, detrending and filtering eddy covariance time series. In: *Handbook of Micrometeorology: A Guide for Surface Flux Measurements* (eds. Lee, X., Massman, W., and Law, B.). Kluwer Academic press, Dordrecht, The Netherlands, pp. 7-31.
- Monson, R. K., Turnipseed, A. A., Sparks, J. P., Harley, P. C., Scott-Denton, L. E., Sparks, K., and Huxman, E., 2002. Carbon sequestration in a high-elevation, subalpine forest. *Global Change Biology* 8, 459-478.
- Moore, T. R., and Dalva, M., 1993. The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. *Journal of Soil Science* 44, 651-664.
- Moya, I., Camenen, L., Evain, S., Goulas, Y., Cerovic, Z. C., Latouche, G., Flexas, J., and Ounis, A., 2004. A new instrument for passive remote sensing: I. Measurements of sunlight induced chlorophyll fluorescence. *Remote Sensing of Environment* 91, 186-197.
- Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G., and Nemani, R. R., 1997. Increased plant growth in the northern latitudes from 1981 to 1991. *Nature* 386, 698-702.
- Nobel, P. S., 1999. *Physicochemical and environmental plant physiology*. Academic Press, San Diego, California, The United States.
- Ögren, E., 1997. Relationship between temperature, respiratory loss of sugar and premature dehardening in dormant Scots pine seedlings. *Tree Physiology* 17, 47-51.
- Oker-Blom, P., Pukkala, T., Kuuluvainen, T., 1989. Relationships between radiation interception and photosynthesis in forest canopies – effect on stand structure and latitude. *Ecological Modelling* 49, 73-87.
- Öquist, G., and Huner, N. P. A., 2003. Photosynthesis of overwintering evergreen plants. *Annual Review of Plant Biology* 54, 329-355.
- Paul, E. A., and Clark, F. E., 1989. *Soil microbiology and biochemistry*. Academic Press, San Diego, The United States. 273 pp.
- Piao, S., Friedlingstein, P., Ciais, P., Viovy, N., and Demarty, J., 2007. Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades. *Global Biogeochemical Cycles* 21, GB3018, doi:10.1029/2006GB002888.
- Piao, S., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luyssaert, S., Margolis, H., Fang, J., Chen, A., Grelle, A., Hollinger, D., Laurila, T., Lindroth, A., Richardson, A. D., and Vesala, T., 2008. Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature* 451, 49-52.
- Porcar-Castell, A., Juurola, E., Ensminger, I., Berninger, F., Hari, P., and Nikinmaa, E., 2008a. Seasonal acclimation of photosystem II in *Pinus sylvestris*. II. Using the rate constants of sustained thermal energy dissipation and photochemistry to study the effect of light environment. *Tree Physiology* 28, 1483-1491.

- Porcar-Castell, A., Juurola, E., Nikinmaa, E., Berninger, F., Ensminger, I., and Hari, P., 2008b. Seasonal acclimation of photosystem II in *Pinus sylvestris*. I. Estimating the rate constants of sustained thermal energy dissipation and photochemistry. *Tree Physiology* 28, 1475-1482.
- Portner, H., Bugmann, H., and Wolf, A., 2009. Temperature response functions introduce high uncertainty in modelled carbon stocks in cold temperature regions. *Biogeosciences Discussion* 6, 8129-8165.
- Rannik, Ü., Keronen, P., Hari, P., and Vesala, T., 2004. Estimation of forest-atmosphere CO<sub>2</sub> exchange by eddy covariance and profile techniques. *Agricultural and Forest Meteorology* 126, 145-155.
- Ricciuto, D. M., Butler, M. P., Davis, K. J., Cook, B. D., Bakwin, P. S., Andrews, A., and Teclaw, R. M., 2008. Causes of interannual variability in ecosystem-atmosphere CO<sub>2</sub> exchange in a northern Wisconsin forest using a Bayesian model calibration. *Agricultural and Forest Meteorology*, 309-327.
- Richardson, A. D., Hollinger, D. Y., Burba, G. B., Davis, K. J., Flanagan, L. B., Katul, G. G., Munger, J. W., Ricciuto, D. M., Stoy, P. C., Suyker, A. E., Verma, S. B., and Wofsy, S. C., 2006. A multi-site analysis of random error in tower-based measurements of carbon and energy fluxes. *Agricultural and Forest Meteorology* 136, 1-18.
- Santaren, D., Peylin, P., Viovy, N., and Ciais, P., 2007. Optimizing a process-based ecosystem model with eddy-covariance flux measurements: A pine forest in southern France. *Global Biogeochemical Cycles* 21, doi:10.1029/2006GB002834.
- Sasai, T., Okamoto, K., Hiyama, T., and Yamaguchi, Y., 2007. Comparing terrestrial carbon fluxes from the scale of a flux tower to the global scale. *Ecological Modelling* 208, 135-144.
- Schaberg, P. G., Wilkinson, R. C., Shane, J. B., Donnelly, J. R., and Cali, P. F., 1995. Winter photosynthesis of red spruce from three Vermont seed sources. *Tree Physiology* 15, 345-350.
- Sellers, P. J., 1985. Canopy reflectance, photosynthesis and transpiration. *International Journal of Remote Sensing* 6, 1335-1372.
- Sellers, P. J., Berry, J. A., Collatz, G. J., Field, C. B., and Hall, F. G., 1992. Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sensing of Environment* 42, 187-216.
- Sellers, P. J., Los, S. O., Tucker, C. J., Justice, C. O., Dazlich, D. A., Collatz, G. J., and Randall, D. A., 1996. A revised land surface parameterization (SiB2) for atmospheric GCMs. Part II: The generation of global fields of terrestrial biophysical parameters from satellite data. *Journal of Climate* 9, 706-737.
- Sellers, P. J., Mintz, Y., Sud, Y. C., and Dalcher, A., 1986. A simple biosphere model (SiB) for use within general circulation models. *Journal of the Atmospheric Sciences* 43, 505-531.
- Sevanto, S., Suni, T., Pumpanen, J., Grönholm, T., Kolari, P., Nikinmaa, E., Hari, P., and Vesala, T., 2006. Wintertime photosynthesis and water uptake in a boreal forest. *Tree Physiology* 26, 749-757.
- Shibistova, O., Lloyd, J., Zrazhevskaya, G., Arneth, A., Kolle, O., Knohl, A., Astrakhantceva, N., Shijneva, I., and Schmerler, J., 2002. Annual ecosystem respiration budget for a *Pinus sylvestris* stand in central Siberia. *Tellus* 54B, 568-589.
- Slayback, D. A., Pinzon, J. E., Los, S. E., and Tucker, C. J., 2003. Northern hemisphere photosynthetic trends 1982-99. *Global Change Biology* 9, 1-15.
- Smolander, S., and Stenberg, P., 2003. A method to account for shoot scale clumping in coniferous canopy reflectance models. *Remote Sensing of Environment* 88, 363-373.
- Snyder, P. K., Delire, C., and Foley, J. A., 2004. Evaluating the influence of different vegetation biomes on the global climate. *Climate Dynamics* 23, 279-302.
- Solantie, R., 1990. The climate of Finland in relation to its hydrology, ecology and culture. *Finnish Meteorological Institute Contributions* 73, Helsinki, Finland, 130 pp.

- Solantie, R., 2004. Daytime temperature sum – a new thermal variable describing growing season characteristics and explaining evapotranspiration. *Boreal Environment Research* 9, 319-333.
- Stenberg, P., Palmroth, S., Bond, B. J., Sprugel, D. G., and Smolander, H., 2001. Shoot structure and photosynthetic efficiency along the light gradient in a Scots pine canopy. *Tree Physiology* 21, 805-814.
- Stryer, L., 1995. *Biochemistry*. W.H. Freeman and Company, The United States. 1064 pp.
- Stull, R. B., 1988. *An Introduction to Boundary Layer Meteorology*. Kluwer Academic Publishers, Dordrecht, The Netherlands. 666 pp.
- Suni, T., Berninger, F., Markkanen, T., Keronen, P., Rannik, Ü., and Vesala, T., 2003. Interannual variability and timing of growing-season CO<sub>2</sub> exchange in a boreal forest. *Journal of Geophysical Research* 108, 4265, doi:10.1029/2002JD002381.
- Taiz, L., and Zeiger, E., 1998. *Plant Physiology*. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, The United States. 792 pp.
- 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., Arneth, A., Shibistova, O., and Lloyd, J., 2003. Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring. *Global Change Biology* 9, 1410-1426.
- Thornley, J. H. M., 2002. Instantaneous canopy photosynthesis: Analytical expressions for sun and shade leaves based on exponential light decay down the canopy and an acclimated non-rectangular hyperbola for leaf photosynthesis. *Annals of Botany* 89, 451-458.
- Thornley, J. H. M., and Johnson, I. R., 1990. *Plant and crop modelling*. Clarendon Press, London, 668 pp.
- Thum, T., Aalto, T., Laurila, T., Aurela, A., Cuntz, M., Kattge, J., and Reick, C., 2009. Modelling effect of frost on carbon dioxide gas exchange in northern boreal coniferous forest. *Geophysical Research Abstracts*, Vol. 11, EGU2009-8447. EGU General Assembly 2009.
- Trudinger, C. M., Raupach, M. R., Rayner, P. J., Kattge, J., Liu, Q., Pak, B., Reichstein, M., Renzullo, L., Richardson, A. D., Roxburgh, S. H., Styles, J., Wang, Y. P., Briggs, P., Barrett, D., and Nikolova, S., 2007. OptiC project: An intercomparison of optimization techniques for parameter estimation in terrestrial biogeochemical models. *Journal of Geophysical Research* 112, G02027, doi:10.1029/2006JG000367.
- Trumbore, S., 2006. Carbon respired by terrestrial ecosystems – recent process and challenges. *Global Change Biology* 12, 141-153.
- Tuomi, M., Vanhala, P., Karhu, K., Fritze, H., and Liski, J., 2008. Heterotrophic soil respiration – Comparison of different models describing its temperature dependence. *Ecological Modelling* 211, 182-190.
- Tuzet, A., Perrier, A., and Leuning, R., 2003. A coupled model of stomatal conductance, photosynthesis and transpiration. *Plant, Cell and Environment* 26, 1097-1116.
- Venäläinen, A., and Nordlund, A., 1988. Kasvukauden ilmastotiedotteen sisältö ja käyttö (Contents and use of the climatological report of a growing season, in Finnish). *Finnish Meteorological Institute Reports* 1988:6, Finnish Meteorological Institute, Helsinki. 63 p.
- Verbeeck, H., Samson, R., Granier, A., Montpied, P., and Lemeur, R., 2008. Multi-year model analysis of GPP in a temperate beech forest in France. *Ecological Modelling* 210, 85-103.
- Vesala, T., Haataja, J., Aalto, P., Altimir, N., Buzorius, G., Garam, E., Hämeri, K., Ilvesniemi, H., Jokinen, V., Keronen, P., Lahti, T., Markkanen, T., Mäkelä, J. M., Nikinmaa, E., Palmroth, S., Palva, L., Pohja, T., Pumpanen, J., Rannik, Ü., Siivola, E., Ylitalo, H., Hari, P., and Kulmala, M., 1998. Long-term field measurements of atmosphere-surface interactions in boreal forest combining forest ecology, micrometeorology, aerosol physics and atmospheric chemistry. *Trends in Heat, Mass and Momentum Transfer* 4, 17-35.
- Vesala, T., Launiainen, S., Kolari, P., Pumpanen, J., Sevanto, S., Hari, P., Nikinmaa, E., Kaski, P., Mannila, H., Ukkonen, E., Piao, S., and Ciais, P., 2009. Autumn warming and carbon balance of a boreal Scots pine forest in Southern Finland. *Biogeosciences Discussion* 6,

7053-7081.

- Vesala, T., Suni, T., Rannik, Ü., Keronen, P., Markkanen, T., Sevanto, S., Grönholm, T., Smolander, S., Kulmala, M., Ilvesniemi, H., Ojansuu, R., Uotila, A., Levula, J., Mäkelä, A., Pumpanen, J., Kolari, P., Kulmala, L., Altimir, N., Berninger, F., Nikinmaa, E., and Hari, P., 2005. Effect of thinning on surface fluxes in a boreal forest. *Global Biogeochemical Cycles* 19, doi:10.1029/2004GB002316.
- Villar, R., Held, A. A., and Merino, J., 1994. Comparison of methods to estimate dark respiration in the light in leaves of two woody species. *Plant Physiology* 105, 167-172.
- Villar, R., Held, A. A., and Merino, J., 1995. Dark leaf respiration in light and darkness of an evergreen and a deciduous plant species. *Plant Physiology* 107, 421-427.
- Wang, K. Y., 1996. Canopy CO<sub>2</sub> exchange of Scots pine and its seasonal variation after four-year exposure to elevated CO<sub>2</sub> and temperature. *Agricultural and Forest Meteorology* 82, 1-17.
- Wang, K. Y., Kellomäki, S., and Laitinen, K., 1996. Acclimation of photosynthetic parameters in Scots pine after three-year exposure to elevated CO<sub>2</sub> and temperature. *Agricultural and Forest Meteorology* 82, 195-217.
- Wang, Y. P., Baldocchi, D., Leuning, R., Falge, E. and Vesala T., 2006. Estimating parameters in a land-surface model by applying nonlinear inversion to eddy covariance flux measurements from eight FLUXNET sites. *Global Change Biology* 12, 1-19.
- Waring, R. H., and Running, S. W., 2007. *Forest Ecosystems: analysis at multiple scales*. Elsevier Science & Technology, The United States, 420 pp.
- Wilson, K. B., Baldocchi, D., and Hanson, P. J., 2001. Leaf age affects the seasonal pattern of photosynthetic capacity and net ecosystem exchange of carbon in a deciduous forest. *Plant, Cell and Environment* 24, 571-583.
- Wilson, K. B., Goldstein, A., Falge, E., Aubinet, M., Baldocchi, D., Berbigier, P., Bernhofer, C., Ceulemans, R., Dolman, H., Field, C., Grelle, A., Ibrom, A., Law, B. E., Kowalski, A., Meyers, T., Moncrieff, J., Monson, R., Oechel, W., Tenhunen, J., Valentini, R., and Verma, S., 2002. Energy balance closure at FLUXNET sites. *Agricultural and Forest Meteorology* 113, 223-243.
- Williams, M., Richardson, A. D., Reichstein, M., Stoy, P. C., Peylin, P., Verbeeck, H., Carvalhais, N., Jung, M., Hollinger, D. Y., Kattge, J., Leuning, R., Luo, Y., Tomelleri, E., Trudinger, C. and Wang, Y.-P., 2009. Improving land surface models with FLUXNET data. *Biogeosciences* 6, 1341-1359.
- Williams, M., Schwarz, P. A., Law, B. E., Irvine, J., and Kurpius, M. R., 2005. An improved analysis of forest carbon dynamics using data assimilation. *Global Change Biology* 11, 89-105.
- Wu, Y., Brashers, B., Finkelstein, P. L., and Pleim, J. E., 2003. A multilayer biochemical dry deposition model, 1. Model formulation. *Journal of Geophysical Research* 108, 4013-4025.
- Wullschleger, S. D., 1993. Biochemical limitations to carbon assimilation in C<sub>3</sub> plants – A retrospective analysis of the A/C<sub>i</sub> curve from 109 species. *Journal of Experimental Botany* 44, 907-920.
- Xu, L., and Baldocchi, D., 2003. Seasonal trends in photosynthetic parameters and stomatal conductance of blue oak (*Quercus douglasii*) under prolonged summer drought and high temperature. *Tree Physiology* 23, 865-877.
- Yuan, F., Arain, M. A., Barr, A. F., Black, A., Bourque, C. P.-A., Coursolle, C., Margolis, H. A., McCaughey, J. H., and Wofsy, S. F., 2008. Modelling analysis of primary controls on net ecosystem productivity of seven boreal and temperate coniferous forests across a continental transect. *Global Change Biology* 14, 1765-1784.