BOREAL ENVIRONMENT RESEARCH 14 (suppl. A): 19–28 © 2009
ISSN 1239-6095 (print) ISSN 1797-2469 (online) Helsinki 27 April 2009

Predicting boreal conifer photosynthesis in field conditions

Pertti Hari[1)], Heikki Hänninen[2)], Frank Berninger[3)], Pasi Kolari[1)],
Eero Nikinmaa[1)] and Annikki Mäkelä[1)]

[1)] *Department of Forest Ecology, P.O. Box 27, FI-00014 University of Helsinki, Finland*
[2)] *Plant Biology, Department of Biological and Environmental Sciences, P.O. Box 65, FI-00014 University of Helsinki, Finland*
[3)] *Chaire en productivité forestière, Departement des sciences biologiques, Université du Québec à Montréal, Montréal QC, H3C 3P8, Canada*

Received 14 Mar. 2008, accepted 2 Mar. 2009 (Editor in charge of this article: Jaana Bäck)

Hari, P., Hänninen, H., Berninger, F., Kolari, P., Nikinmaa, E. & Mäkelä, A. 2009: Predicting boreal conifer photosynthesis in field conditions. *Boreal Env. Res.* 14 (suppl. A): 19–28.

Automatic continuous monitoring of shoot-level gas exchange and environmental factors in natural conditions provides an efficient but unexploited tool for testing the predictive power of plant photosynthesis models. We used automatically operated measurement chambers to monitor the CO_2 exchange of Scots pine (*Pinus sylvestris*) shoots in Finnish Lapland near the timberline over two growing seasons, yielding a total of 90 000 measurements. In this paper, we show that a recent ecophysiological model predicts the daily and seasonal pattern of photosynthesis with the unbiased percentages of explained variance of 90% and 92%, respectively, utilising temporally independent data. Our model combines the optimal stomatal control model of photosynthesis with a model of annual cycle of photosynthesis. The key feature for applications of the model is the temperature driven onset, acceleration and decline of photosynthesis. With these dynamics, the model provides a useful tool for analysing the effects of climate change on annual photosynthetic production in boreal conifers.

Introduction

Monitoring of shoot- or leaf-level gas exchange together with the driving environmental factors in natural conditions during the whole growing season provides an efficient way to study the ecophysiology of plant photosynthesis. The main advantage of this approach is that it facilitates long-term documentation of gas exchange taking place in natural conditions, thus providing comprehensive data for developing and testing models of photosynthesis. With this approach we can study the underlying physiological regularities, which generate the observed daily and annual patterns of photosynthesis. This method, however, is little utilized at present, perhaps because it requires building quite massive and expensive measuring setups in field conditions (Hari *et al.* 1994, Granat and Richter 1995, Vesala *et al*. 1998, Miyama *et al*. 2003, Hari and Kulmala 2005, Medhurst *et al*. 2006).

Mäkelä *et al.* (2004) presented an ecophysiological model for analyzing the dynamics of photosynthesis of boreal coniferous trees. Their model was constructed by synthesizing two previous models, each addressing a different aspect of photosynthesis. First, *the optimal stomatal control model* describes the momentary environmental responses of photosynthesis and the acclimation of photosynthesis to drought (Hari *et al*. 1986). Its underlying principle is to address the trade-off involved in the functioning of stomata, i.e. the loss of water necessarily linked to the uptake of carbon (Cowan and Farquhar 1977). Second, *the annual cycle model of photosynthesis* introduces the effect of the biochemical regulation system on photosynthesis during the annual cycle (Pelkonen 1980, Pelkonen and Hari 1980, Bergh *et al*. 1998, Hari *et al*. 2008).

The ultimate aim of scientific research is to discover permanent regularities in nature. The common praxis in the research of photosynthesis is to collect a rather limited data set and to fit a quite complicated model to the data. This leads to two complications in discovering permanent regularities; (i) the estimation of the parameter values introduces bias into the fit of the model, such that the proportion of explained variance is too high, and (ii) the stability of the regularity remains open. The possibilities to study permanent regularities are greatly improved if the data set is large and if it covers a long time span.

The combined model of Mäkelä *et al*. (2004) predicted the seasonal course of the daily photosynthetic production well, the percentage of explained variance being 89.6. In the study of Mäkelä *et al*. (2004), however, data for 1997 only were available, so it was not possible to expose the model to a stringent test in a temporally independent data set, nor to analyse the estimation bias. In the present study, the data for 1998 and 1999 will be used to analyze the stability of the regularities discovered with the data from 1997. As temporally independent data are used, this will allow a test of the predictive power of the model without estimation bias.

Material and methods

The model of photosynthesis

The optimal stomatal control model

The optimal stomatal control model of photosynthesis applied here (Hari *et al*. 1986, Mäkelä *et al*. 1996, 2004, Hari and Mäkelä 2003) is derived from a set of simplifying assumptions using the optimality paradigm introduced by Cowan and Farquhar (1977). The solution results in a model of gas exchange which consists of equations for stomatal conductance, g (m s^{-1}), rate of photosynthesis, A (mol CO$_2$ m^{-2} s^{-1}), and rate of transpiration, E (mol H$_2$O m^{-2} s^{-1}), as functions of photosynthetically active radiation, I (mol m^{-2} s^{-1}), carbon dioxide concentration, C_a (mol CO$_2$ m^{-3}), saturation deficit of water vapour, D (mol H$_2$O m^{-3}), respiration r (mol CO$_2$ m^{-2} s^{-1}) and the cost of transpiration, λ (mol CO$_2$ (mol H$_2$O)$^{-1}$):

$$A(t)=\frac{\left[g(t)C_{\mathrm{a}}+r\right]f\left(I(t)\right)}{g(t)+f\left(I(t)\right)} \tag{1}$$

$$E(t) = ag(t)D(t) \tag{2}$$

$$g_{\mathrm{s}}(t)=\left[\sqrt{\frac{C_{\mathrm{a}}-\dfrac{r}{f\left(I(t)\right)}}{\lambda a D(t)}}-1\right]f\left(I(t)\right) \tag{3}$$

$$g=\begin{cases} g_{\min}, \text{ if } g_{\mathrm{s}} \le g_{\min} \\ g_{\mathrm{s}}, \quad \text{if } g_{\min} \le g_{\mathrm{s}} \le g_{\max}, \\ g_{\max}, \text{ if } g_{\mathrm{s}} \ge g_{\max} \end{cases} \tag{4}$$

where $g_{\min}$ (m s^{-1}) is the cuticular conductance, $g_{\max}$ (m s^{-1}) is the stomatal conductance for CO$_2$ when the stomata are fully open, and a is the ratio of diffusivity of water relative to carbon dioxide.

The function f introducing saturation of biochemical reactions is

$$f(I)=\frac{\alpha\gamma I}{\alpha I+\gamma}, \tag{5}$$

where γ (m s^{-1}) is the saturation level of $f(I)$ (m s^{-1}) and α (m^3 mol^{-1}) is the initial slope of the function.

Equations 1 and 3 include a respiration term for the CO$_2$ released in the mesophyll due to the metabolism of cells. It depends on temperature like all biochemical reactions. Exponential temperature dependence is commonly observed to provide a satisfactory fit with measurements. We assume that

$$r(T_l)=r_0 Q_{10}^{T_l/10}, \tag{6}$$

where T_l (°C) is leaf temperature, and r_0 and Q_{10} are parameters.

Apart from the respiration term, leaf temperature is also present in the model through the water vapor saturation deficit, D. The mesophyll is assumed to be saturated with water vapour at a given leaf temperature, and the water vapour concentration in the ambient air is measured. Leaf temperature is not necessarily the same as the air temperature measured by the monitoring system. While convection reduces the temperature difference from leaf to ambient air, the difference tends to increase due to solar radiation and decrease due to transpiration. The wind speed inside the chamber is constant, thus convection is proportional to the difference between ambient and leaf temperature. The bending of the needles into a plane (Hari and Mäkelä 2003) reduces the efficiency of convectional heat transport. The heating by solar radiation is the dominant factor in the energy balance of the needle. The leaf temperature was approximated from chamber temperature with a simple linear relationship

$$T_l = T_a + bI, \tag{7}$$

where T_a is the air temperature in the chamber and b (°C mol^{-1} m^2 s) is a parameter introducing the effect of light on leaf temperature (Mäkelä *et al* 2004).

The model of annual cycle

The annual cycle of metabolism is reflected in seasonal changes in the parameter values of the light-response curve, α and γ (Eq. 5). Furthermore, the two parameters change in proportion, such that the shape of the light-response remains constant but its level changes during the year. By using a modified version of the model of Pelkonen and Hari (1980), Mäkelä *et al*. (2004) showed that the seasonal changes could be explained as dynamic acclimation to prevailing temperatures, using the concept of *state of photosynthetic acclimation*, S (°C). It is an aggregated measure of the state of those physiological processes of the leaves that determine the current photosynthetic capacity at any moment of time, and it is formulated through the following dynamic equation:

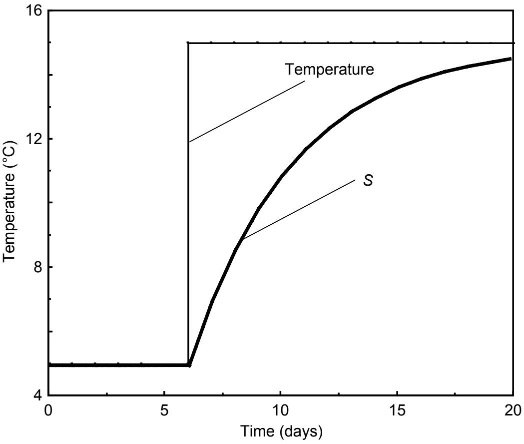

Fig. 1. Illustration of the slow response of the state of acclimation S to stepwise temperature increase from 5 °C to 15 °C. The time constant in the calculation is 5 days.

$$\frac{dS}{dt} = \frac{1}{\tau}\left(T_l - S\right), \tag{8}$$

where τ (hours) is a time constant and T_l (°C) is leaf temperature. According to this, S follows leaf temperature, T_l, in a delayed manner: if T_l is held constant S approaches T_l, and if T_l is changed, S will start to move towards the new temperature with a time constant τ. The response of S to step-wise temperature change from 5 °C to 15 °C is demonstrated in Fig. 1. S changes rather rapidly during the first days of the temperature change and the response levels out in about 15 days.

Mäkelä *et al*. (2004) presented evidence that there is a linear relationship between the parameter α (i.e. the initial slope of the photosynthetic light response) in the optimal stomatal control model and S:

$$\alpha(S) = \max\,\{c_1(S - S_0), 0\}, \tag{9}$$

where S_0 (°C) is a threshold value of the state of acclimation and c_1 is a coefficient of proportionality. Similarly, γ depends on S through its linear dependence on α. This formulation is similar to that by Pelkonen and Hari (1980) who defined the state of acclimation through a more complicated differential equation but essentially driven by temperature similarly to the present model.

Data

The data was measured at SMEAR I (Station For Measuring Ecosystem Atmosphere Relations) in Finnish Lapland (67°46´N, 29°35´E) 200 km north of the Arctic Circle. The monitoring system consists of three trap-type acrylic chambers (3.6 dm^3), a tubing system, infrared gas analyzers for CO$_2$ and water vapour, sensors for photosynthetically active radiation and temperature and a micro computer for control and online recording of the measurements. The chambers close automatically for measurements for a period of 60 s, approximately 120 times a day. In the cuvette there is an electric fan keeping airflow through the chamber at 0.5 m s^{-1} when open, and mixing the air when closed. During the 60 s measurement periods, a pump draws air into the gas analyzers at a flow rate 0.017 dm^3 s^{-1}. The infrared gas analyzers (URAS 3 G, Hartmann & Brown, Germany) for CO$_2$ and water vapour measure concentrations at intervals of ten seconds during the closure of the chamber. The CO$_2$ exchange was determined from the mass balance equation utilising concentration differences and fluxes between the chamber and ambient air. Photosynthetically active radiation (PAR) is monitored outside the chamber with a Li-Cor sensor (LI-190, LI-COR Ltd., NE, USA), and temperature inside the chamber with a thermocouple. The system is almost identical to that at SMEAR II, a monitoring station in southern Finland, which has been described in detail by Hari *et al*. (1999). The accuracy of the gas exchange measurements is about 2% (Hari *et al*. 1999).

Three trees were chosen for measurements in an even-aged Scots pine stand on top of a shallow-sloped hill near the SMEAR I monitoring tower at 395 m a.s.l. The timberline occurs in this area at about 400 m a.s.l. The stand has regenerated naturally in the early 1950s, with current stand density of about 1000 trees ha^{-1} and dominant height 8 m. The chambers were attached on the southern side of the treetops at about 7.5 m from the ground. One shoot was chosen for monitoring in each tree. The current buds were removed in order to keep the needle area as stable as possible, and needles were bent to a plane so they would have the same geometry as the light sensor.

The measurements of CO$_2$ exchange are not performed during winter because of strong ice formation. In 1998 we started the chamber measurements on 27 April (there was about 1 m of snow then) and ended them on 23 September. The number of measurements per day was 120. A technical problem in the pneumatic system operating the chambers caused a long measuring break at midsummer and thunderstorms lead to occasional missing days, resulting in a total of 33 missing days. The number of measurements in 1998 was over 42 000. In 1999 the chamber measurements continued from 9 May to 30 September, with 120 measurements per day. The measuring system operated very well during the summer 1999 since only two days were excluded from the analysis due to technical problems. The total number of measurements was over 51 000.

Estimation of shoot-specific parameters

The photosynthetic machinery is the same in all needles in a pine tree, thus the model should, in principle, be able to predict the CO$_2$ exchange for all shoots in the canopy throughout the years. There are, however, some shoot-specific features such as damage in the needles, shading within shoot and the nutritional status of the needles. Among the parameters of the model, λ in Eq. 3 and c_1 in Eq. 9 represent these shoot-specific features. Therefore, it was necessary to calibrate the model to the shoots used in the monitoring, i.e. for both 1998 and 1999 the values of these two shoot-specific parameters were estimated for each of the three shoots being monitored using the measurements carried out during that particular year. For both of these years we selected a six-day period, which included both sunny and cloudy weather to estimate the values of the shoot-specific parameters with the normal procedure of minimising the residual sum of squares. The days utilised in the estimation were rejected when testing the model to avoid estimation bias in the proportion of explained variance. The other nine parameters of the model are not shoot-specific, so they were fixed to the values previously estimated on the basis of the monitoring during 1997 at the same field station (Mäkelä *et al*. 2004; Table 1).

Results and discussion

Severe testing of theories and models is essential to the progress of research. However, the conclusions in the ecophysiological research are quite often based on rather limited data sets. The results are obtained with a statistical treatment of the measurements. Then a model, often derived from the data, is fitted into the data by minimizing the residual sum of squares. This procedure often results in a rather good agreement between the measured and modeled values of the examined variables. However, when using this procedure an estimation bias is introduced into the results. The estimation makes the fit of the model seemingly too good and any systematic difference between measurements and model prediction is a sign of insufficient statistical analysis. The real test of the model, on the contrary, is to compare the prediction of the model with a new temporally independent data set that was not used in the estimation of the values of the model parameters. However, this kind of severe testing is exceptional in plant ecophysiological research.

Our data set is large, consisting of 90 000 measurements of CO_2 exchange, photosynthetically active radiation, temperature, atmospheric CO_2 and water vapor concentration. The large number of measurements enables severe testing of our model and identification of shortcomings in the approach for further development. The predictive power of the model is the key characteristic in the evaluation of the model, so that high predictive power indicates support for the model. Any discrepancies between measurements and the prediction of the model indicate problems in one or several phases of the approach; so the factors generating the discrepancy should be carefully analyzed and evaluated.

In the daily patterns of photosynthetic rate two major phenomena were apparent. First, the photosynthetic rates were much lower at the beginning of the photosynthetically active period (i.e. in May), than later during the summer (i.e. in July and August) (Fig. 2). Secondly, as revealed by the good fit between observation and prediction, the shape of the daily pattern of photosynthetic rate was caused by both the daily pattern of PAR and the degree of stomatal control. During cloudy days with little or no stomatal control the fit between prediction and observation was good, without exception (Fig. 2B). The fit was also quite good on days with intermittent cloudiness (Fig. 2C). During sunny days with a strong stomatal control the prediction was also generally successful but in a few cases the fit was less good (Fig. 2A). However, despite the few shortcomings (Fig. 2A) the model predicted the daily patterns of photosynthetic rate well, the percentages of explained variance (PEV) without estimation bias being 94% and 88% for 1998 and 1999, respectively.

The daily photosynthetic production followed a clear seasonal pattern (Fig. 3). Large

Table 1. Values of the parameters applied in the testing of the model of photosynthesis. Parameters γ and c_1 are shoot-specific. The values the other parameters were fixed to the ones obtained previously with data measured in 1997 (Hari and Mäkelä 2003, Mäkelä *et al*. 2004) not used in the present study for model testing.

Parameter	Unit	Symbol	Value	Equation
Cost of transpiration	mol CO_2 (mol H_2O)$^{-1}$	λ	0.0023*	3
Ratio of γ to α	µmol PAR m^{-2} s^{-1}		1600	5
Ratio of H_2O to CO_2 diffusion constants		a	1.6	2
Minimum conductance (cuticular)	m s^{-1}	g_{min}	0.000075	4
Maximum conductance (stomata fully open)	m s^{-1}	g_{max}	0.005	4
Increase in leaf temperature per unit PAR	°C (µmol)$^{-1}$ m^2 s	b	0.008	7
Coefficient of leaf respiration	mol CO_2 m^{-2} s^{-1}	r_0	0.091	6
Relative increase of respiration per 10 °C		Q_{10}	2.3	6
Time constant of delayed response to ambient temperature	h	τ	330	8
Threshold value of running mean temperature at which photosynthesis starts	°C	T_0	–4.5	9
Ratio of α to state of acclimation	m^3 mol^{-1} °C	c_1	0.040*	9

* Mean of all shoots.

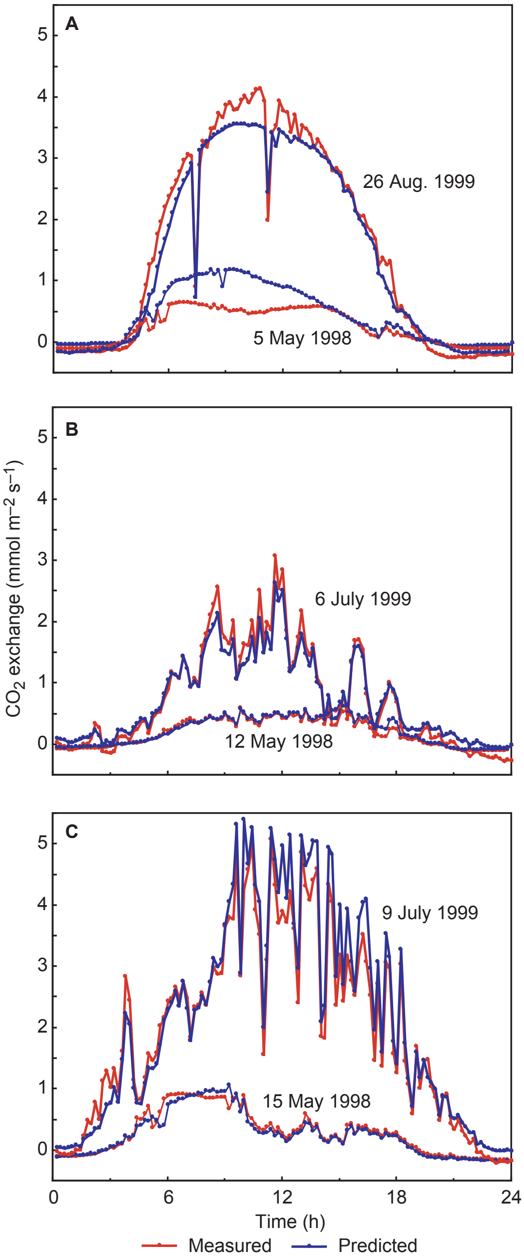

Fig. 2. Measured and predicted daily patterns of photosynthetic rate of shoots of Scots pine growing in Finnish Lapland. In each panel the lower curves represent a day slightly after the onset of the photosynthetically active period in the spring and the upper curves a day during the summer. Each curve represents either the measured photosynthetic rate of one experimental shoot or the corresponding rate predicted by a model of conifer photosynthesis (Hari and Mäkelä 2003, Mäkelä *et al.* 2004). The panels show examples of (**A**) sunny days, (**B**) cloudy days, and (**C**) days with intermittent cloudiness.

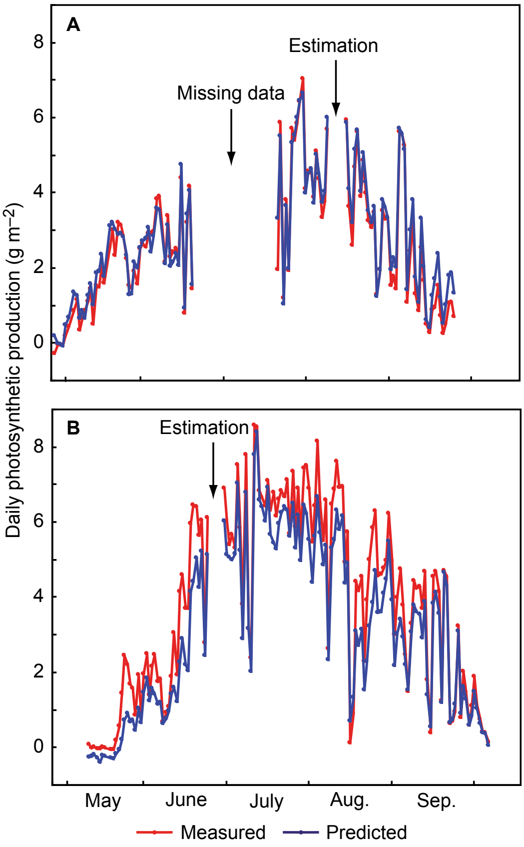

Fig. 3. Measured and predicted seasonal patterns of daily photosynthetic production of shoots of Scots pine growing in Finnish Lapland in (**A**) 1998 and (**B**) 1999. Each curve represents either the mean calculated with three measured experimental shoots or the mean calculated with the corresponding predictions of a model of conifer photosynthesis (Hari and Mäkelä 2003, Mäkelä *et al.* 2004). The gaps in the data denoted by 'Estimation' refer to data used in the estimation of shoot-specific parameters and thus excluded from the model testing (*see* Material and methods). The other gap in the data for 1998 ('Missing data') was caused by technical failures in the automatic monitoring of carbon exchange.

year-to-year variation was visible in the timing of recovery of the photosynthesis. In 1998 the recovery commenced in early May (Fig. 2A) whereas in 1999 it began almost one month later (Fig. 3B). Similarly to the daily patterns of photosynthetic rate (Fig. 2), the model also predicted accurately the seasonal pattern of daily photosynthetic production. Despite the slight inaccuracy in predicting the recovery in 1999 (Fig. 3B), the seasonal pattern of daily photosynthetic production was predicted well, the percentages of explained variance (PEV) without estimation bias being 93% and 92% for 1998 and 1999, respectively (Fig. 3). This indicates a high predictive power of the model. As far as we know, no such test of models of photosynthesis has previously been carried out with temporally independent data.

There were some systematic differences between measured and predicted CO_2 exchange during sunny days, especially in the spring (Fig. 2A). As indicated by the high values of PEV, these cases were quite rare in the test, but still the reason for the discrepancies should be analysed. The reason may be systematic measuring errors, erroneous parameter values or shortcomings in the model structure. The light and temperature measurements are very vulnerable to external disturbances. Our light sensor was located outside the chamber and it may have had dirt on the sensing plate. The sensor also omits the shading effect of the chamber on the shoot. We measured air temperature with thermocouples inside the chamber. These sensors may introduce systematic measuring error of about 1 °C. In addition, the approximation of needle temperature (Eq. 7) introduces inaccuracies into the results.

The prediction was based on fixed parameter values. This seems to be justified in most cases, but there is some evidence suggesting that the parameter λ has higher values early in the spring than later in the summer. This phenomenon occurs nearly every spring, but at that time there are quite few sunny days when the phenomenon can be seen. The effect of the discrepancy on the predictive power of the model is small because the phenomenon is so rare. Thus, we applied the important methodological principle of parsimony, so that we did not introduce the relationship between λ and S into the model.

All models are idealizations of the reality, so they should be developed in order to better describe the reality. Our model is based on several idealizing assumptions and its structure is simple. However, in the present study the model passed successfully the severe test with temporally independent data, and the observed discrepancies between the observation and model prediction can be explained by measuring errors or higher values of the parameter λ in the spring than later during summer. Improvements of the quality of the measurements are needed for the development of the model.

The research of the annual cycle of photosynthesis has long traditions in the research group at the Department of Forest Ecology in Helsinki University. Hari *et al* 1970 introduced the state of development in the analysis of daily shoot elongations of Scots pine. Pelkonen (1980) and Pelkonen and Hari (1980) expanded the use of the state of development into the analysis of the annual cycle of photosynthesis. Hari and Mäkelä (2003) and Mäkelä *et al*. (2004) combined the annual cycle of photosynthesis with the optimal stomatal control model of photosynthesis. They also replaced the state of development with a new term state of acclimation. These models have been very usefull in the analysis of the effects of annual cycle on photosynthesis and shoot elongation. The physiological basis has, however, remained unclear.

The introduction of the state of functional substances (Hari *et al* 2008) was a clear step forward in the understanding of the annual cycle of photosynthesis. The Scots pine, like other evergreens in boreal forests, has to tolerate very low temperatures and yet, it has to be able to fully utilise the favourable short summer. Biochemical regulation synchronise the alternating tolerant and intolerant states with the annual cycle of light and temperature. Important parts of developing tolerant state are increasing elasticity of the cell membranes and concentrations of substances that avoid freezing of living cells (Pearce 2001). During these conditions of no growth, and slow ability of carbon assimilation in dark reactions due to low temperatures, also the light harvesting system develops permanent changes in pigments that decrease the interception of excess light and increase its dissipation as heat (Savich *et al*. 2002, Porcar-Castell 2008). Biochemical regulation changes the concentrations and activities of pigments, membrane pumps and enzymes to match the conditions created by variation in the light and temperature in a synchronized way. The overall outcome of these changes is also reflected on the rate of photosynthesis. Thus there are regularities in the functional substances during the annual cycle. The concept state of functional substances was introduced to describe these regularities and it was described with a scalar variable S called as the state of the functional substances.

Several models for the different aspects of photosynthesis have previously been presented, including the biochemical reactions (Farquhar *et al.* 1980, Farquhar and von Caemmerer 1982), stomatal conductance (Collatz *et al.* 1991, Dewar 2002), and annual cycle of metabolism (Pelkonen and Hari 1980, Bergh *et al.* 1998), and they have also been tested in various combinations against field data and eddy covariance data (Law *et al.* 2000, Kramer *et al.* 2002). The present study is unique in the sense that at the same time (1) the model combines all these processes, (2) the data set is extensive, allowing us to test for both seasonal behaviour and the faster processes simultaneously, (3) we are predicting CO_2 exchange during two summers without estimation bias instead of fitting the model to the measured data, and (4) the proportion of explained variance in the prediction with temporally independent data was high.

In all three aspects of the model, it appears to be simpler than other widely used models. For example, the Farquhar model requires more than ten parameters to describe the biochemical light and dark reactions as compared with five parameters in the present model. Similarly, the annual cycle model is only driven by one external variable with two parameters as compared with the eight parameters and two temperature variables required by the model by Bergh *et al.* (1998). The simplicity reduces the need for input data and makes the simultaneous estimation of parameters more rigid by reducing the possible cross-correlations between the parameter values. Moreover, the Farquhar model has been shown to perform similarly to the optimal stomatal control model after the completion of spring recovery (Aalto *et al.* 2002), and the seasonal model has been shown to provide similar predictions to the model of Bergh *et al.* (1998) (Hänninen and Hari 2002). This suggests that for long-term predictions, the fine detail of the model may not be as essential as its ability to incorporate realistically the interplay between different types of impact at the relevant time scales.

Our findings demonstrate the benefits of long-term monitoring of photosynthesis at leaf or shoot level. The data produced by leaf and shoot measurements is more informative to study photosynthesis than the commonly used micrometeorological flux measurements (Kramer *et al.* 2002, Suni *et al.* 2003) which do not separate between plant photosynthesis and soil respiration as components of the observed net gas exchange.

In conclusion, the present results demonstrate that our model accounts for the most essential underlying physiological regularities that generate the observed complicated patterns of photosynthesis in the real world. At short time scales within one day, photosynthetic rate is largely driven by changes in photosynthetically active radiation and water vapour saturation deficit, whereas the temperature-driven onset, acceleration and decline of photosynthesis dominate the long-term temporal patterns in photosynthesis since the value of the parameter α slowly increases from 0 to its summer time value. The slow change in photosynthetic capacity over the seasons confirms that changes in the concentrations and activities of pigments, enzymes and other substances involved in photosynthesis play important role in the annual cycle of photosynthesis in addition to direct response of biochemical process rates to light and temperature. Thus it is essential to address the environmental responses of photosynthesis simultaneously at two different temporal scales, as an instantaneous response to the driving factors, and as a slow change along the annual cycle of trees. This approach will be useful in studies of photosynthesis of tree canopies (Bergh *et al.* 1998, Medlyn *et al.* 2003), forest growth (Landsberg 2003, Mäkelä 2003), and finally the global carbon cycle (Black *et al.* 2000, Buchmann 2002). As our model predicts the temperature-driven seasonal dynamics of photosynthesis, it also provides a tool for research of the effects of the predicted climate change on annual photosynthetic production of boreal coniferous trees. Our analysis indicates that our model is able to capture essential features of the permanent regularities in photosynthesis of Scots pine in field conditions.

Acknowledgements: This study was funded by the Helsinki University Environmental Research Centre (HERC) and by the Academy of Finland Center of Excellence program (project no. 1118615).

References

Aalto T., Hari P. & Vesala T. 2002. Comparison of an optimal stomatal regulation model and a biochemical model in explaining CO_2 exchange in field conditions. *Silva Fennica* 36: 615–623.

Bergh J., McMurtrie R.E. & Linder S. 1998. Climatic factors controlling the productivity of Norway spruce: a model-based analysis. *Forest Ecology and Management* 110: 127–139.

Black T.A., Chen W., Barr A.G., Arain M.A., Chen Z., Nesic Z., Hogg E.H., Neumann H.H. & Yang P.C. 2000. Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophysical Research Letters* 27: 1271–1274.

Buchmann N. 2002. Plant ecophysiology and forest response to global change. *Tree Physiology* 22: 1177–1184.

Collatz G.J., Ball J.T., Grivet C. & Berry J.A. 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agricultural and Forest Meteorology* 54: 107–136.

Cowan I.R. & Farquhar G.D. 1977. Stomatal function in relation to leaf metabolism and environment. *Symposia of the Society for Experimental Biology* 31: 471–505.

Dewar R.C. 2002. The Ball-Berry-Leuning and Tardieu-Davies stomatal models: synthesis and extension within a spatially aggregated picture of guard cell function. *Plant Cell and Environment* 25: 1383–1398.

Farquhar G.D. & von Caemmerer S. 1982. Modelling of photosynthetic response to environmental conditions. In: Lange O.L., Nobel P.S., Osmond C.B. & Ziegler H. (eds.), *Encyclopedia of plant physiology*, vol. 12, Springer Verlag, New York, pp. 549–587.

Farquhar G.D., von Caemmerer S. & Berry J.A. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta* 149: 78–90.

Granat L. & Richter A. 1995. Dry deposition to pine of sulphur dioxide and ozone at low concentration. *Atmospheric Environment* 29: 1677–1683.

Hänninen H. & Hari P. 2002. Recovery of photosynthesis of boreal conifers during spring: a comparison of two models. *Forest Ecology and Management* 169: 53–64.

Hari P. & Kulmala M. 2005. Station for measuring ecosystem–atmospere relations (SMEAR II). *Boreal Environment Research* 10: 315–322.

Hari P. & Mäkelä A. 2003. Annual pattern of photosynthesis of Scots pine in the boreal zone. *Tree Physiology* 23: 145–155.

Hari P., Mäkelä A., Korpilahti E. & Holmberg M. 1986. Optimal control of gas exchange. *Tree Physiology* 2: 169–175.

Hari P., Keronen P., Bäck J., Altimir N., Linkosalo T., Pohja T., Kulmala M. & Vesala T. 1999. An improvement of the method for calibrating measurements of photosynthetic CO_2 flux. *Plant Cell and Environment* 22: 1297–1301.

Hari P., Kolari P., Bäck J., Mäkelä A. & Nikinmaa E. 2008. Photosynthesis. In: Hari P. & Kulmala L. (eds.), *Boreal forest and climate change*, Springer Verlag, Dordrecht, pp. 231–242.

Hari P., Kulmala M., Pohja T., Lahti T., Siivola E., Palva L., Aalto P., Hämeri K., Vesala T. & Pulliainen E. 1994. Air pollution in eastern Lappland: challenge for an environmental measurement station. *Silva Fennica* 28: 29–39.

Hari P., Leikola M. & Räsänen P. 1970. A dynamic model of the daily hight increment of plants. *Annles Botanici Fennici* 7: 375–378.

Kramer K., Leinonen I., Bartelink H.H., Berbigier P., Borghetti M., Bernhofer Ch., Cienciala E., Dolman A.J., Froer O., Gracia C.A., Granier A., Grünwald T., Hari P., Jans W., Kellomäki S., Loustau D., Magnani F., Markkanen T., Matteucci G., Mohren G.M.J., Moors E., Nissinen A., Peltola H., Sabaté S., Sanchez A., Sontag M., Valentini R. & Vesala T. 2002. Evaluation of six process-based forest growth models using eddy-covariance measurements of CO_2 and H_2O fluxes at six forest sites in Europe. *Global Change Biology* 9: 213–230.

Landsberg J. 2003. Modelling forest ecosystems: state of the art, challenges, and future directions. *Canadian Journal of Forest Research* 33: 385–397.

Law B.E., Waring R.H., Anthoni P.M. & Abers J.D. 2000. Measurements of gross and net ecosystem productivity and water vapour exchange of a *Pinus ponderosa* ecosystem, and evaluation of two generalized models. *Global Change Biology* 6: 155–168.

Mäkelä A. 2003. Process-based modelling of tree and stand growth: towards a hierarchical treatment of multi-scale processes. *Canadian Journal of Forest Research* 33: 398–409.

Mäkelä A., Berninger F. & Hari P. 1996. Optimal control of gas exchange during drought. *Annals of Botany* 77: 461–467.

Mäkelä A., Hari P., Berninger F., Hänninen H. & Nikinmaa E. 2004. Acclimation of photosynthetic capacity in Scots pine to the annual cycle of temperature. *Tree Physiology* 24: 369–376.

Medhurst J., Parsby J., Linder S., Wallin G., Ceschia E. & Slaney M. 2006. A whole-tree chamber system for examining tree-level physiological responses of field-grown trees to environmental variation and climate change. *Plant Cell and Environment* 26: 1853–1869.

Medlyn B., Barrett D., Landsberg J., Sands P. & Clement R. 2003. Conversion of canopy intercepted radiation to photosynthate: review of modelling approaches for regional scales. *Functional Plant Biology* 30: 153–169.

Miyama T., Kominami Y., Tamai K., Nobuhiro T. & Goto Y. 2003. Automated foliage chamber method for long-term measurement of CO_2 flux in the uppermost canopy. *Tellus B* 55: 322–330.

Pearce R. 2001. Plant freezing and damage. *Annals of Botany* 87: 417–424.

Pelkonen P. 1980. The uptake of carbon dioxide in Scots pine during spring. *Flora* 169: 386–397.

Pelkonen P. & Hari P. 1980. The dependence of the springtime recovery of CO_2 uptake in Scots pine on temperature and internal factors. *Flora* 169: 398–404.

Porcar-Castell A., Bäck J., Juurola E. & Hari P. 2008. Short-term acclimation of photosynthetic light reactions to light. In: Hari P. & Kulmala L. (eds.), *Boreal forest and climate change*, Springer Verlag, Dordrecht, pp. 248–255.

Savitch L.V., Leonardos E.D., Krol M., Jansson S., Grodzinski B., Huner N.P.A. & Öquist G. 2002. Two different strategies for light utilization in photosynthesis in relation to growth and cold acclimation. *Plant Cell Environment* 25: 761–771.

Suni T., 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. & Lloyd J. 2003. Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring. *Global Change Biology* 9: 1410–1426.

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., Nikinmaa E., Palmroth S., Palva L., Pohja T., Pumpanen J., Rannik Ü., Siivola E., Ylitalo H., Hari P. & 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.