Carbon Dioxide Exchange of Scots Pine Shoots as Estimated by a Biochemical Model and Cuvette Field Measurements

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A biochemical model was used to calculate CO_2 fluxes to Scots pine shoots in two boreal measurement stations, Hyytiälä in southern Finland (61°51'N, 24°17'E) and Värriö in northern Finland (67°46'N, 29°35'E). The results of the model were compared with cuvette measurements performed in field conditions. A differential equation for change in gas concentration inside a closed cuvette was constructed and solved in order to obtain conductances and fluxes. The results were generally in a good agreement, the correlation coefficients varied from 0.74 to 0.95. Some discrepancies were also found. The model followed more intensively changes in temperature. This could be seen in northern Finland measurements at low temperatures (<18 °C). The modelled temperature response indicated low fluxes at low temperatures, but measurements did not show any decrease. The irradiation response was relatively similar in both measuring sites and according to the model. Cuvette measurements showed slightly smaller quantum yields as a result from shading of the needles. The temperature dependences of the biochemical model parameters J_{max} and $V_{c(max)}$ were re-evaluated from the field measurements. The results for $V_{c(max)}$ agreed well with earlier estimations, while the results for J_{max} indicated relatively high values at low temperatures especially in northern Finland. Exponential fitting produced also substomatal concentrations of CO_2, which agreed quite well with the model. The daily minimum of substomatal/ambient concentration ratio varied from 0.4 to 0.8.

Keywords photosynthesis, CO_2 exchange, cuvette measurements, *Pinus sylvestris*, Scots pine
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1 Introduction

The CO_2 assimilation rate of leaves depends on several environmental and physiological parameters (i.e. light regime, nutrition and water stress). They cause changes in stomatal conductance and the photosynthetic capacity of leaves. Photosynthetic capacity is often explained by a biochemical model which combines studies of enzyme kinetics and electron transport to whole leaf gas exchange. Conductance can also be linked to photosynthetic capacity (e.g. Leuning 1995). Biochemically based models of photosynthesis have been utilized in many large scale studies of ecosystem productivity (e.g. Ågren et al. 1991, McMurtrie and Wang 1993, Baldocchi and Harley 1995, Harley and Baldocchi 1995, Lloyd et al. 1995, Kellomäki and Väisänen 1997). Exact formulation varies from model to model, but they can be dated back to original work by Farquhar et al. (Farquhar, von Caemmerer and Berry 1980, von Caemmerer and Farquhar 1981, Farquhar and von Caemmerer 1982).

This study is also based on the original work by Farquhar et al., which was re-parametrized for Scots pine (*Pinus sylvestris*) by Wang et al. (1996). The aim of the study was to find the level of agreement between the modelled results and cuvette measurements of Scots pine gas exchange performed in field conditions at two measuring sites located in northern and southern Finland (both in sub-arctic regime). Differences along the N-S geographical gradient are quite probable (e.g. Berry and Björkman 1980, Troeng and Linder (1982), Luoma 1997). The cuvette measurements were performed on basis of continuous monitoring throughout the growing season. Their implementation was therefore as simple and as easy as possible to attend. The parameters of the biochemical model for Scots pine CO_2 assimilation are based on gas exchange measurements in at least a partly controlled environment, and it is interesting to know how well the model agrees with field measurements using simple equipment designed for continuous monitoring. This information is needed also in many plant-atmosphere transfer models which are often based on the leaf gas exchange model and the scaling of it on shoot and canopy levels. There are few field measurements of CO_2 assimilation of Scots pine that utilize the biochemical model (e.g. Hällgren et al. 1990, Wang 1996a).

The measurements considered in this study were performed using a trap-type cuvette system. Differential equations for change in CO_2 and H_2O concentrations inside a closed cuvette were constructed and solved. A common and simple equation for flux, $F = g(c - c_i)$, was applied to determine conductances (g) and substomatal concentrations (c_i) for each measurement period by exponential fitting. The values for maximum electron transport rate J_{max} and maximum carboxylation rate $V_{c(max)}$ were estimated from the field measurements and some general considerations of the sensitivity of the biochemical model to changes in parameters were also performed.

2 Materials and Methods

The measurement set-up is introduced in the following. The method for processing time series of the cuvette measurement data and its validity are also discussed and the biochemical model used for estimating exhange rates is briefly introduced.

2.1 Measurement Set-up

Gas exchange of Scots pine needles was calculated from the cuvette measurements during the summer of 1996 in the Värriö (67°46'N, 29°35'E, 390 m a.s.l.) and Hyytiälä (61°51'N, 24°17'E, 181 m a.s.l.) environmental measuring stations. The measuring systems were quite similar in both stations and were a result of several years of research and development by the personnel on the stations and in the University of Helsinki (Haataja and Vesala 1997). The systems consisted of trap-like cuvettes, pipelines for gas flow, a pneumatic system for controlling cuvettes, magnetic valves and a mass flow controller for gas flows, gas analyzers and air pumps for gas flow and a compressor for the pneumatic system. The systems were controlled by a computer (Fig. 1).

A pine shoot (150–250 needles) was installed inside a cylindrical acryl-plastic trap type cu-

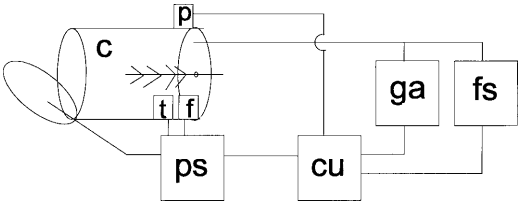

Fig. 1. Schematic representation of the measuring system. c = cuvette, f = fan, t = thermoelement, p = light sensor and ps = pneumatic system for closing and opening the lid of the cuvette. The system consists of pneumatic cylinder, magnetic valves and air compressor. ga = gas analyzers, consisting of analyzers for H_2O and CO_2 (in Hyytiälä also separate sample line for NO_x, SO_2 and O_3), flow rate controller, air pump and magnetic valves for choosing the measurement mode. fs = flush flow system for flushing the sample line between measurements. The system consists of magnetic valves, flow meter and controllers and air pump. cu = controlling unit consisting of data logger and microcomputer.

vette through a hole in the bottom. A fan stirred the air while the cuvettes were alternately closed and opened. The cuvette was small (3.5 dm^3) in order to achieve the best possible sensitivity for changes in gas concentrations. The small size of the cuvette resulted in increasing temperatures during period of closing and thus the cuvette had to be opened again. Short closing times and results from empty reference cuvettes showed, that otherwise the cuvette conditions remained near ambient ones also during measurements. The surrounding air was allowed to gradually enter into the cuvette also during measurements so that the outgoing and incoming mass flows were equal. The air flows were balanced so that no pressure drop occurred inside the cuvette and, on the other hand, environmental disturbances (wind gusts etc.) did not affect the measurements. The lid was closed for 70 s once every 10 minutes at Värriö and once every 25 minutes at Hyytiälä. The change in gas concentrations was registered once in every ten seconds in Värriö and once in every five seconds in Hyytiälä when the lid was closed. The air was transported to the gas analyzers by heated stainless steel pipes. There was

Table 1. Installation and projected needle area of pine shoots in selected cuvettes at the measuring stations.

Cuvette	Needle area [m^2]	Setting
Värriö 0	0.0542	flat
Värriö 1	0.0274	flat
Värriö 2	0.0129	free
Hyytiälä 0	0.0272	free
Hyytiälä 5	0.0441	flat

a constant flow of air through the pipes also between measurements (flush flow, see Fig. 1) in order to avoid condensation of water and exchange of CO_2 with the walls of the tubing. CO_2 and H_2O concentrations were measured with Hartmann & Braun URAS 4 infrared absorption analyzers in both stations. Calibration and pressure corrections were performed for each measurement. The cuvettes were installed in the top of the trees (no shading) and the shoots consisted of one- and two-year-old needles. The shoots were flattened in some of the cuvettes, i.e. the needles were forced into the horizontal position with help of thin strings. This construction enabled more reliable estimates of the radiation incident to needles. Needles were collected during autumn 1996 and the total needle surface area for each shoot was determined. The total area was divided by π in order to obtain a projected needle area (e.g. Stenberg, 1995). A short description of each cuvette used in this work is presented in Table 1.

Temperature (CuKo thermoelements) was measured both inside and outside and PAR, photosynthetically active radiation (LiCor 190 SB sensors), just outside the cuvette. At Hyytiälä SO_2, NO_x and O_3 concentrations were also measured from the cuvette. A variety of meteorological and other forest ecological measurements were also performed at the stations (Haataja and Vesala 1997, Hari et al. 1994, Ahonen et al. 1997).

2.2 Processing the Cuvette Measurements

2.2.1 Curve Fitting Procedure

The time series of CO_2 and H_2O cuvette measurements were processed by using curve fitting procedures. An exponential equation was fitted to the gas concentration measurements for each period of time when the cuvette was closed. The equation is a solution to following differential equation describing the functioning of the cuvette and pine shoot inside it. Change in the gas concentration in the closed cuvette can be expressed in the following way:

$$BV_{cuv}\frac{\partial c}{\partial t} = Bc_{amb}Q - BcQ - FA_{needle} \quad (1)$$

where c is the concentration inside the cuvette, c_{amb} is the concentration in the ambient air, F is the flux into the needle, Q is the flow rate and V_{cuv} is the volume of the cuvette. $B = P_{amb}/(RT_K)$ is here just to convert concentrations explained in Table 2 into right units (μmol m^{-3}). The first term in the right describes the flux of ambient air into the cuvette, the second is the sample flux from the cuvette and third is the flux into the needles (per sq. meter, if multiplied with needle area A_{needle}).

The flux F can be expressed as $F = g(c - c_i)$ (e.g. Nobel, 1991), where g is the conductance of the transferring gas. The conductance was assumed to stay constant through 70 seconds while the cuvette was closed. The intercellular concentration c_i can be expressed as $c_i = Kc$, a fraction of the concentration outside the needle. The factor K was also assumed to be constant through the period of closing. For carbon dioxide the flux F_c can be expressed as

$$F_c = g(c - c_i) = g_c(1 - K)c = g'_c\, c \quad (2)$$

For water vapour the flux F_w is simple to formulate, since the walls of the substomatal cavity can be assumed to be covered with water (e.g. Nobel 1991) and the intercellular concentration is the saturated concentration of water vapour:

$$F_w = g_w\left(c_{H_2O} - \frac{p_{sat,H_2O}}{p_{amb}}\right) \quad (3)$$

The saturation vapour pressure of water was calculated from $p_{sat,H2O} = \exp(77.345 - 7235.4/T_K - 8.2\ln(T_K) + 0.0057113T_K)$, where T_K is the ambient air temperature in Kelvins (fitted to the experimental data of Landoldt-Börnstein, 1960).

The intercellular concentration of CO_2 can now be solved from the fitted conductances for CO_2 and H_2O and taking account differences in diffusivities:

$$c_i = c(1 - 1.6g'_c/g_w) \quad (4)$$

Numerical analyses were made using *Matlab* (version 5.0). The packages used in fitting procedures utilized the Nelder-Mead simplex search algorithm for minimizing functions of several variables and the golden section search and parabolic interpolation algorithm for minimizing functions of one variable.

2.2.2 Quality of the Exponential Fitting

During the measurement period CO_2 concentrations in the closed cuvette decrease due to assimilation by the needle. There is also input of CO_2 from the ambient air. The simplest approach is to estimate flux F into the needle from two measurement points near cuvette closing time, but here F was calculated by exponential fitting to all measurement points during the period of closing, which describes better the actual change in concentration and allows a more exact determination of fluxes, conductances and substomatal concentration of CO_2. Using exponential fitting, the flux F to the needle was first assumed to be constant for the time the cuvette was closed, 70 seconds (Eq. 1). In the second stage F was assumed to obey the well known equation $F = g(c - c_i)$ (e.g. Nobel 1991), where g is the conductance of the transferring gas (Eq. 2). The conductance was assumed to stay constant through 70 seconds while the cuvette was closed, which is a better choice than assuming a constant flux while cuvette concentrations are changing. Also the effect of the replacement air (term $c_{amb}Q$ in Eq. 1) was investigated. It is possible that there are also fluxes that are independent of ambient concentration, or the dependence is of other form than Eq. 2 (E.g. non-photorespiratory respiration). To study this,

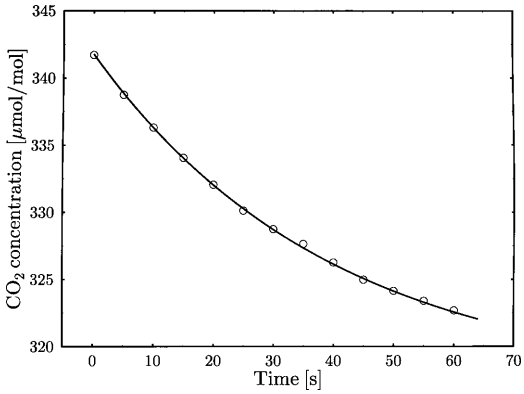

Fig. 2. An example of one series of daytime CO_2 concentration measurements inside a closed cuvette at Värriö. The curve is obtained by exponential fitting with constant conductance assumption.

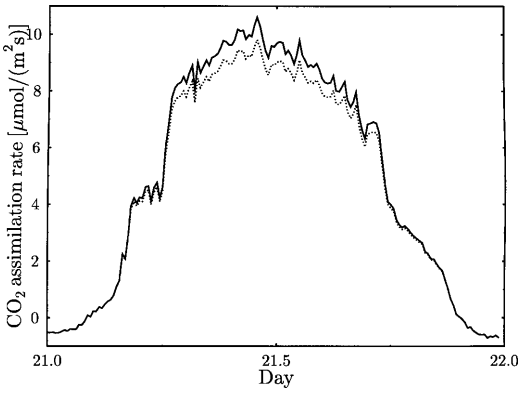

Fig. 3. The CO_2 assimilation rate during 20.7.1996 in Värriö as estimated by two methods: Solid line: Constant conductance assumption in exponential fitting. g'_c was multiplied with first concentration in a closed cuvette to obtain the flux. Dotted line: Constant flux assumption in exponential fitting.

an additional term independent of concentration was temporarily added to Eq. 2.

The concentration of carbon dioxide decreased by a maximum of 15 % at Värriö and Hyytiälä when the cuvette was closed. The corresponding increase in water vapour concentration was max. 30 %. This might have resulted in difficulties in fitting the values, but in practise it did not have any clear effect on the results. According to Hendrey et al. (1997) short term CO_2 fluctuations may affect photosynthetic efficiency and also long-term photosynthesis, if the duration of the oscillation is 1 minute or more. Nevertheless, the magnitude of the oscillation in studies by Hendrey et al. (1997) was considerably larger (550 ppm) than changes in one measurement cycle cuvette concentration (50 ppm) in our measurements and the oscillation was carried out by a step-change method. Changes in cuvette concentration were thus unlikely to cause long-term changes in photosynthetic processes.

The temperature in the cuvette changes during closure by a maximum of 2 °C. This brings noise in the results, but the effect is unimportant here. Small errors in estimations of the cuvette volume and flow rate are also of minor importance. The CO_2 flux is inversely proportional to the assimilating needle area, and it is the most effective and uncertain parameter in the flux estimations. The curve fitting usually produced good results. This was especially seen during daytime (Fig. 2) while during change from net assimilation to net production of CO_2 the results (and measurements) were more ambiguous. Each exponential curve-fitted concentration differed from the measured concentration by a certain percentage during one cycle (70s). These percentages can be averaged over the cycle to obtain an average error. The error for carbon dioxide measurements had a maximum of 4 % when considering all cycles, but usually it was below 0.5 %. Water vapour measurements were more noisy and errors of more than 10 % were occasionally observed, but usually the error was below 2 %. Curve fittings with large errors were abandoned (= 1–2 % of the total number of the measurements). Water vapour measurements during periods of rain were also abandoned (= 20–30 % of measurements).

The results of the constant flux and constant conductance assumptions were in accordance with each other (Fig. 3). The fitting procedure using the constant conductance assumption produced a factor which could be multiplied with concentration to obtain the flux during each measurement. When it was multiplied with mean concentration during closure the result was the same as with the constant flux assumption, which is realistic since the ‘constant flux’ corresponds to

actual mean flux during the period of closing. This also brings evidence for the reliability of the constant conductance assumption. The additional concentration-independent term, 'zero flux' (or respiration), produced only unclear values oscillating around zero. It did not make the results better. The term $c_{amb}Q$ due to leakage had to exist in the equation, otherwise the results were not reasonable.

2.3 Biochemical Model

CO_2 assimilation rates were also predicted with a biochemical model parametrized for Scots pine grown in southern Finland conditions (Wang et al. 1996). The model is based on the original work by Farquhar et al. in the early 80's (Farquhar, von Caemmerer and Berry 1980, von Caemmerer and Farquhar 1981, Farquhar and von Caemmerer 1982). According to Wang et al. (1996) the carbon dioxide assimilation rate can be expressed as

$$A = \min(A_c, A_j) \tag{5}$$

where A_c is the Rubisco-limited rate

$$A_c = V_{c(\max)} \frac{K_o c_i - 0.105 K_c c_{O_2}}{K_c c_{O_2} + K_c K_o + K_o c_i} - R_d \tag{6}$$

and A_j is the RuP_2-regeneration limited rate

$$A_j = J \frac{K_o c_i - 0.105 K_c c_{O_2}}{4.5 K_o c_i + 1.1025 K_c c_{O_2}} - R_d \tag{7}$$

c_i is the concentration of CO_2 in the chloroplast, c_{O2} is the concentration of O_2 in the chloroplast, $V_{c(max)}$ is maximum rate of carboxylation with non-limiting RuP_2, J is the potential electron transport rate, R_d is the rate of non-photorespiratory respiration, K_c is the Michaelis-Menten constant for CO_2 and K_o is the Michaelis-Menten constant for O_2. Temperature dependences of K_c and K_o were adopted from Farquhar et al. (1980).

The dependence of J on irradiance can be written as (Wang et al. 1996, Farquhar and Wong 1984)

$$\Theta J^2 - (Iq - J_{\max})J - qIJ_{\max} = 0 \tag{8}$$

where I is irradiance, J_{max} is the maximum rate of electron transport, q is the effectivity factor for the use of light and Θ is the convexity factor of the curve (Table 2).

The functional forms of temperature dependences of $V_{c(max)}$, J_{max} and R_d were first adopted from Wang et al. (1996):

$$J_{\max}, V_{c(\max)} = \frac{\exp(C_{Tn} - \Delta H_{an} / [RT_K])}{1 + \exp([\Delta S_n T_K - \Delta H_{dn}] / [RT_K])} \tag{9}$$

$$R_d = \exp(C_{Tn} - \Delta H_{an} / [RT_K]) \tag{10}$$

During the dark period, R_d was multiplied by a factor 1.45. The constants were re-evaluated from estimations for J_{max}, $V_{c(max)}$ and R_d by Wang et al. (1996) at five different temperatures, since there seemed to be some confusion in their resulting parameters. Values for constants are presented in Table 3.

The temperature dependencies for $V_{c(max)}$ and J_{max} were also re-estimated from the Värriö and Hyytiälä measurements. Following functional forms were used (Lloyd et al. 1995):

$$V_{c(\max)} = V_{c(\max)298} \exp\left[\left(\frac{\Delta H_{an}}{298.15R}\right)\left(1 - \frac{298.15}{T_K}\right)\right] \tag{11}$$

$$J_{\max} = \frac{B_J \exp[\Delta H_{an}(T_K / 298.15 - 1) / (RT_K)]}{1 - \exp[(\Delta S_n T_K - \Delta H_{dn}) / (RT_K)]} \tag{12}$$

For values of constants see Table 3. The validity of the new parametrizations for $V_{c(max)}$ and J_{max} was checked by statistical χ-tests (e.g. Barlow 1988). The quantity χ^2 is the squared difference between the observed values and their theoretical predictions, weighted by the errors of the measurement.

The stomatal conductance is needed to solve the substomatal concentration of CO_2. The substomatal concentration can be estimated directly from the flux measurements using the method presented in Eqs. 1–4. This method was utilized when some biochemical model parameters were re-estimated, but first the conductance and substomatal concentrations were calculated using a simple, widely used method as modified by Wang

Table 2. Values (at 25 °C), units and definitions of parameters for Equations 1–13. [1] from Wang et al. (1996), [2] estimated from Värriö and Hyytiälä measurements and [3] from Farquhar et al. (1980).

Definition	Symbol and units	Value
CO_2 assimilation rate	A(μmol m^{-2}s^{-1})	
Rubisco-limited rate of assimilation	A_c(μmol m^{-2}s^{-1})	
RuP_2-regeneration limited rate of assimilation	A_j(μmol m^{-2}s^{-1})	
Needle area	A_{needle}m^2	see Table 1
CO_2 concentration in cuvette	c(μmol mol^{-1})	
CO_2 concentration in ambient air	c_{amb}(μmol mol^{-1})	
CO_2 concentration in intercellular spaces	c_i (μmol mol^{-1})	
H_2O concentration in cuvette	c_{H2O}(μmol mol^{-1})	
O_2 concentration	c_{O2}mmol mol^{-1}	210
The difference between $p_{sat,H2O}$ and actual vapour pressure of water in the ambient air at certain T_K	D_v(kPa)	
Flux into unit needle area	F(μmol m^{-2}s^{-1})	
CO_2 flux	F_c(µmol m^{-2}s^{-1})	
H_2O flux	F_w(µmol m^{-2}s^{-1})	
Stomatal conductance	g(mol/m^{2}s)	
Stomatal conductance to CO_2	g_c(mol/m^{2}s)	
g_c multiplied by $(1 - c_i / c)$	g_c'(mol/m^{2}s)	
Stomatal conductance to H_2O	g_w(mol/m^{2}s)	
Minimum stomatal conductance to H_2O	g_0(mol/m^{2}s)	0.047[1]
Empirical coefficient representing the composite sensivity of conductance to A	g_1	3.78[1]
Incident irradiance	I(μmol m^{-2}s^{-1})	
Potential rate of electron transport	J(μmol m^{-2}s^{-1})	
Maximum rate of electron transport	J_{max} (μmol m^{-2}s^{-1})	
Michaelis-Menten constant for CO_2	K_c(μmol mol^{-1})	460[3]
Michaelis-Menten constant for O_2	K_o(μmol mol^{-1})	330 000[3]
Saturation vapour pressure for H_2O	$p_{sat,H2O}$ (Pa)	
Ambient air pressure	P_{amb}(Pa)	
Effectivity factor for the use of light	q	0.29[1](0.14[2])
Sample flow rate	Q(m^3/s)	
Gas constant	R(Jmol^{-1}K^{-1}	8.314
Non-photorespiratory respiration	R_d(µmol m^{-2}s^{-1})	1.0[1]
Temperature	T_K(K)	
Maximum rate of carboxylation	$V_{c(max)}$ (μmol m^{-2}s^{-1})	
Volume of the cuvette	V_{cuv}(m^3)	0.0035
CO_2 compensation point in the absence of non-photorespiratory respiration	Γ_*(μmol mol^{-1})	31
Convexity factor of the light response curve	Θ	0.40[1](0.70[2])

(1996a). Wang (1996a) represented a modified form (eg. Leuning, 1995) of model of Ball et al. (1987) for stomatal conductance to water vapour:

$$g_w = g_0 + g_1 \frac{A}{D_v(c - \Gamma_*)} \quad (13)$$

where g_0 is the minimum stomatal conductance to water vapour, g_1 is an empirical coefficient representing the composite sensivity of conductance to A, D_v is the difference between the saturation vapour pressure of water at temperature T_K and actual vapour pressure of water in the ambient air and c is the CO_2 concentration in the chamber which is assumed to equal the concentration in the leaf surface. The concentration can be slightly lower in the leaf surface due to boundary layer resistance, but the thickness of the

Table 3. Values, units and definitions of parameters for Equations 9–12. [1] estimated from Wang et al. (1996), [2] estimated from Hyytiälä measurements and [3] estimated from Värriö measurements (only for temperatures <20 °C. Above 20 °C J_{max} = 90 μmol m^{2}s^{-1}).

Definition	Symbol and units	For	Values for Eqs. 9 & 10	Values for Eqs. 11 & 12
Activation energy for CO_2 and light-saturated assimilation	ΔH_a(Jmol^{-1})	$V_{c(max)}$ J_{max} R_d	62651[1] 69366[1] 32648[1]	28500[2,3] 42591[2],28093[3]
Energy of deactivation	ΔH_d(Jmol^{-1})	$V_{c(max)}$ J_{max}	148657[1] 151921[1]	 72715[2],58800[3]
Entropy of the denaturation equilibrium of CO_2 and light-saturated assimilation	ΔS(JK^{-1}mol^{-1})	$V_{c(max)}$ J_{max}	494[1] 512[1]	 253[2],214[3]
Constant	C_T	$V_{c(max)}$ J_{max} R_d	29.878[1] 33.716[1] 13.157[1]	
Constant	B_J(μmol m^{-2}s^{-1})	J_{max}		434[2],643[3]
Maximum rate of carboxylation at 25 °C	$V_{c(max)298}$ (μmol m^{-2}s^{-1})	$V_{c(max)}$		62[2,3]

boundary layer is rather difficult to determine for a needle-shaped object (cylinder) in well mixed air (cuvette includes a fan for circulating the air). Thickness of the boundary layer is probably quite small in comparison to other types of leaves. Γ_* is the CO_2 compensation point in the absence of non-photorespiratory respiration. The temperature dependence of Γ_* was adopted from Brooks and Farquhar (1985).

The concentration of CO_2 in the intercellular air spaces was calculated from

$$c_i = c - \frac{1.6A}{g_w} \quad (14)$$

The factor 1.6 converts the conductance for water vapour into conductance for CO_2 according to differences in the diffusivities of these gases in air. c_i is assumed to be equal to the concentration of CO_2 in the sites of carboxylation (Farquhar and von Caemmerer, 1982) so that Equations 5, 13 and 14 can be solved together. Values of parameters in the biochemical model are presented in Tables 2 and 3.

3 Results

Results from the field measurements and corresponding estimations for the CO_2 flux given by the biochemical model are considered in the following. New parametrizations for J_{max} and $V_{c(max)}$ are also introduced.

3.1 Time Series of the Gas Exchange of Needles and Dependences on the Environmental Variables

The measured absolute values for CO_2 assimilation rate differed from the results of the biochemical photosynthesis model by a factor 0.5–2.0 depending on the shoot (An example is shown in Fig. 4). The cuvettes with free twig (Värriö 2, Hyytiälä 0) showed large fluxes compared to the model, whereas the flattened twigs showed smaller fluxes. The maximum flux predicted by the biochemical model is almost exactly 15.0 μmol/m^{2}s for each shoot. When all the results were scaled to same level, the model and measurements were in relatively good agreement. The correlation coefficients between model and meas-

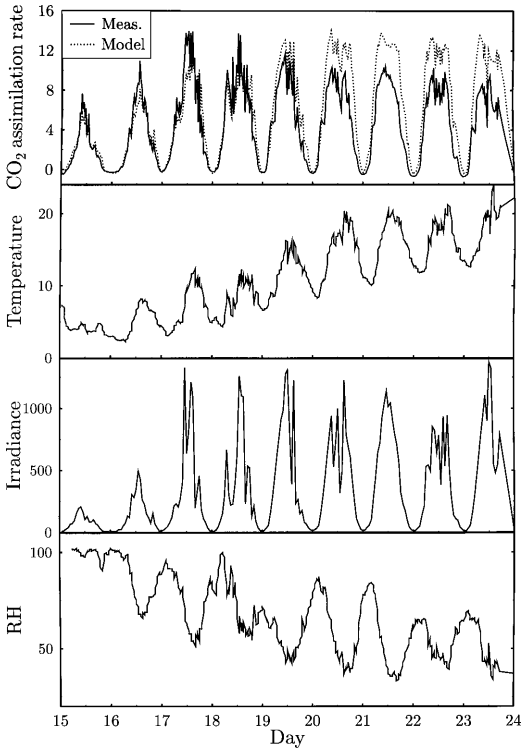

Fig. 4. Some environmental variables and the CO_2 assimilation rate during July 15–23 in Värriö cuvette 0 according to the measurements and biochemical model adjusted for southern Finland conditions. Values are 30 min. averages. Units: CO_2 flux [μmol/(m^{2}s)], Temperature [°C], Irradiance [μmol/(m^{2}s)] and RH [%].

urements varied between 0.74–0.95 (four of the five cuvettes over 0.90). The best agreement was achieved during rainy days while during dry, bright days measured fluxes are lower. In Värriö cuvette 1 the effect of warm and dry days could be most clearly seen in lowered afternoon fluxes and thus the correlation coefficient was smaller. Some effects could also be seen in Värriö 2.

There were some large SO_2 episodes in Värriö during July 1996. On July 29 high concentrations were observed during the whole day (max. over 30 μg/m^3) and on July 31 a short but high episode (max. over 50 μg/m^3) occurred in the morning. These occasional episodes in the otherwise unpolluted air are thought to emanate from industrial sources less than 200 km away (Ahonen et al. 1997). The CO_2 assimilation rate was not observed to decrease relative to the modelled results during these short pollution periods. Of course, as only a few episodes were studied, definite conclusions can not be made and thus further studies are needed.

3.1.1 Responses to Temperature and Relative Humidity

To examine the temperature dependence, results from a few morning-noon hours of each day were chosen. These measurements represented light-saturated fluxes without possible effects of large afternoon water vapour deficits (e.g. Beadle et al. 1985). Results from 7–9.30 am were chosen for Värriö cuvettes 1 and 2 and from 9.30–12.00 for Värriö 0, Hyytiälä 0 and Hyytiälä 5 according to the timing of daily maximum of CO_2 flux in each cuvette. The irradiance was required to be more than 800 μmol/m^{2}s.

According to biochemical photosynthesis model the CO_2 assimilation rate showed a clear dependence on temperature with a maximum at 16–19 °C, as was determined by Wang et al. (1996) (Fig. 5). Cuvette measurements in Hyytiälä agreed relatively well with the model and showed some temperature dependence. Above 18 °C (77 % of observations) the negative correlation with temperature (–0.68) was evident. Agreement with the biochemical model was poor in the Värriö measurements. Measurements did not show a very clear dependence on temperature below 18 °C (some measurements even indicated negative correlations). The correlation between model and measurements was significantly higher when temperatures above 18 °C (only 39 % of observations) were considered. Below 5 °C the assimilation rate decreased clearly, but quantitative estimations were difficult to make. Actual night frosts (studied by e.g. Hällgren et al. 1990) did not occur during the summer. g_0 and g_1 in Eq. 13 may actually be temperature dependent in such a way, that the values are larger in lower temperatures (Eqs. 19 and 20 in Woodward et al. 1995). Anyhow, this change in the biochemical model did not alter

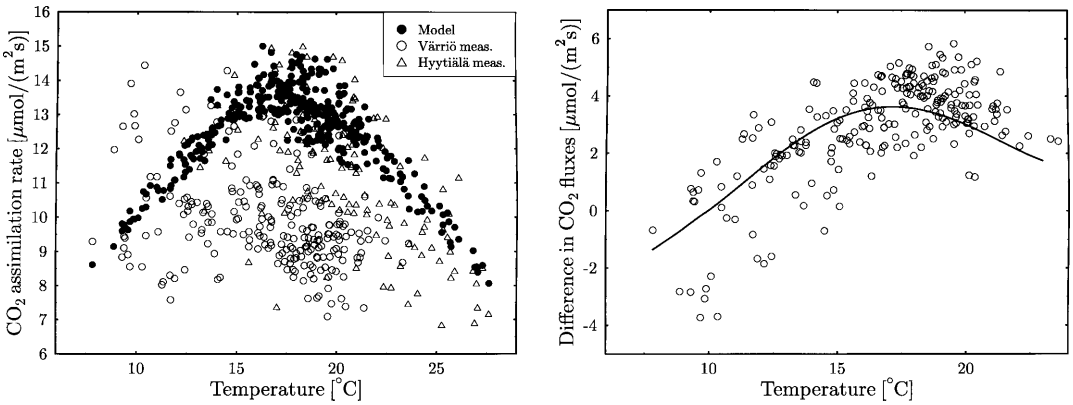

Fig. 5. A Temperature dependence of the daily maximum CO_2 assimilation rate according to biochemical model and measurements at Värriö and Hyytiälä during July 1996. Fluxes are scaled to 15 μmol/(m^{2}s). B Difference between the model and Värriö measurements. Line describes the shape of the model results curve in Fig. 5A. The shape of the difference curve follows closely the modelled curve, which indicates that there is no evident temperature dependence according to the measurements.

Table 4. Correlation coefficients between the daily maximum CO_2 flux and some environmental variables in Värriö cuvette 0 during 15–25.7.1996.

	Model	Measurements
Irradiance – CO_2 flux	0.81	0.78
Temperature – CO_2 flux	0.91	0.26
Relative humidity – CO_2 flux	–0.90	–0.40

the results significantly.

One interesting period from the Värriö measurements was chosen for closer examination (Fig. 4). During July 14–16 there was almost continuous rain. During July 17–23 temperatures increased and relative humidites decreased. Stomatal conductance (calculated from Eq. 3) decreased during early afternoon almost every day and particularly during warm, dry days indicating stomatal closure. During July 15–23 the model indicated first low daytime maximum fluxes which then by increasing temperature and irradiance, rose to a constant level (Fig. 4). The measured daytime fluxes increased steeply following irradiance, and then decreased to a constant level which is lower than that modelled. This could be seen in all the Värriö cuvettes. It seemed that, at least during this period, the model followed temperature variations more intensively than the measurements. Correlation coefficients for the period of daily maximum fluxes (9.30–12a.m. for Värriö 0) showed high correlations with irradiance (Table 4). Correlations with temperature and RH were considerably lower according to the measurements.

3.1.2 Responses to Light Intensity

The CO_2 flux response to light intensity was studied by examining morning measurements from each day. Sunny and cloudy days were considered separately. The typical value for the quantum yield of a C3 plant is around 0.05 (e.g. Nobel 1991), but it changes according to season, temperature and growing conditions (e.g. Wang 1996b). According to cuvette measurements the quantum yield was 0.027 and 0.046 for Värriö 0 (flat) and Hyytiälä 0 (free), respectively. When measurements were scaled in such a way, that the maximum flux from all five cuvettes was 15.0 μmol/m^{2}s, which is almost exactly the maximum flux in all cuvettes according to the biochemical model, the cuvette measurements indicated a quantum yield of 0.025–0.035 (Fig. 6). There were no significant differences between

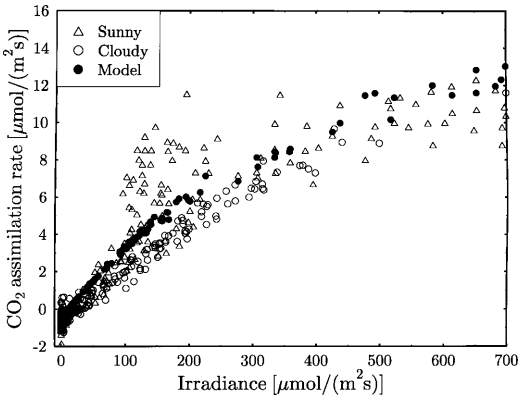

Fig. 6. The irradiation dependence of the CO_2 assimilation rate according to the biochemical model and measurements during bright and cloudy mornings. Fluxes are scaled to 15 μmol/(m^{2}s).

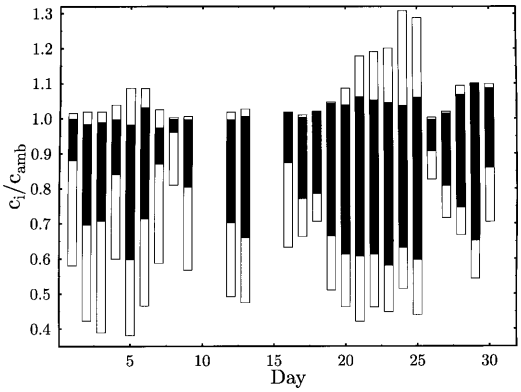

Fig. 7. Ratio of substomatal to ambient CO_2 concentration during July in Värriö cuvette 0. Bars in the figure represent limits of daily variation (from 30 min. averages); large white bars according to the exponential fitting to measurements and smaller black bars according to the biochemical model.

flattened and free shoots, or between Hyytiälä and Värriö measurements. The measured quantum yields are slightly smaller in comparison to the model.

Sunny and cloudy mornings were separated from the research material and the quantum yield was calculated for these two cases. During cloudy mornings radiation is more diffuse and the quantum yield could be higher because PAR measurements better describe the irradiance in needle surfaces. Irradiance varied relatively slowly during the selected cloudy mornings, and thus it could be assumed that CO_2 exchange was able to follow the changes in irradiance. The quantum yield on sunny mornings did not differ from cloudy mornings according to the biochemical model. The measurements showed some differences (Fig. 6). During cloudy mornings the slope was quite orderly. During sunny mornings the curve first followed the cloudy measurements curve but separated at values less than 100 μmol/m^{2}s and formed relatively irregular shapes depending on the cuvette examined. Bright mornings seemed to add more uncertainty into the irradiance vs. assimilation curve. Quantitative differences in quantum yields between sunny and cloudy mornings were rather difficult to estimate on the basis of these measurements.

The substomatal concentration of CO_2 was estimated from the measurements using Eq. 4. It was compared to the substomatal concentration calculated from Eqs. 13–14. The daytime substomatal/ambient concentration was slightly smaller than modelled (Fig. 7). The factor was 0.4–0.8 depending on irradiance conditions etc., while according to the biochemical model it was 0.6–0.9. Some days are missing because of heavy rain and thus unreliable transpiration measurements. During the night c_i/c_{amb} was almost always above one, whereas the biochemical model did not produce as high nighttime concentrations.

3.2 The Temperature Dependences of J_{max} and $V_{c(max)}$

The photosynthesis parameters J_{max} and $V_{c(max)}$ were estimated from the research material. It was assumed that the biochemical model response could be improved (especially in Värriö) if the temperature dependences of J_{max} and $V_{c(max)}$ were re-evaluated. J_{max} and $V_{c(max)}$ are typically expressed as exponential functions of temperature (e.g. Lloyd et al. 1995). Other formulations also appear (e.g. Woodward et al. 1995). $V_{c(max)}$ is typically rising with temperature and J_{max} has a temperature maximum. Here some polynomials

of first and second order were first fitted to the data set in order to simplify the calculation procedure and minimize the number of free parameters. The results obtained using more complex equations were then compared to the simple equations. J_{max} (Eq. 12), $V_{c(max)}$ (Eq. 11), q and Θ (Eq. 8) were considered unknowns that had to be fitted, otherwise the general form of the model (including respiration) was adopted from Wang et al. (1996) (Eqs. 5–7). Conductances and substomatal concentrations of CO_2 were obtained from CO_2 and H_2O measurements as introduced above (from exponential fitting).

$V_{c(max)}$ was obtained from selected midday results of all shoots separately. Results were chosen so that the irradiance was clearly not limiting. First and second order polynomials for $V_{c(max)}$ were used in the model that was fitted into these measurements. Similar results were obtained by using an exponential Equation 11. The functional form of the equation was adopted from Lloyd et al. (1995). Parameters for the equation are described in Tables 2 and 3. All shoots indicated quite similar response to temperature, i.e. $V_{c(max)}$ is constantly increasing with rising temperature. These results are in relatively good agreement with Wang et al. (1996) and other estimates (Wullschleger 1993).

The irradiation dependence (Eq. 8) is described by three parameters q (slope), Θ (curvature) and J_{max} (max. value that the curve is approaching. See also Table 2.). The temperature dependence of J_{max} can be expressed with Equation 12 (Lloyd et al. 1995, Farquhar et al. 1980). The equation for J_{max} together with Eq. 8 contains too many free parameters so that they could be reliably simultaneously estimated from current material. Some estimates were obtained by first fitting q and Θ and after that the temperature dependence of J_{max} expressed as a first or second order polynomial. The result was compared to a simpler but not so easily adjustable equation $J_{\max} = \alpha I / \sqrt{1+\alpha^2 I^2 / J_{\max}^2}$ (e.g. Harley et al. 1986). q and Θ of 0.14 and 0.7 were found to be suitable for this data set, produce good results for J_{max} and also agree with results of the simpler equation with a of 0.13. Low values for q and α result from shading.

Results from all shoots indicated that J_{max} does not get very low values at low temperatures. It was relatively constant or even slightly decreasing with increasing temperature. This is particularly true in Värriö, where the model response is considerably better if J_{max} is allowed to stay high at low temperatures (<18 °C). Hyytiälä measurements required relatively high J_{max} also at high temperatures (>20 °C) and the requirements for low temperatures were not as clear as in Värriö. Several equations of functional form of Eq. 12 (Lloyd et al. 1995, Farquhar et al. 1980) with varying parameters were applied to the model. The best agreement with measured fluxes was obtained using parameters introduced in Table 3.

The validity of the new sets of parameters was studied with statistical χ-tests (Barlow 1988). Calculated χ^2 values represent the difference between measured and modelled fluxes, weighted by the measurement error. The error in the CO_2 flux measurement was estimated to be 5 % of the value of the flux + constant (0.5 μmol/m^{2}s). The χ^2 values obtained using the model with new temperature dependences for J_{max} and $V_{c(max)}$ (Eqs. 11 and 12 and Table 3) were compared to χ^2 obtained using the same model with old temperature dependences (Eq. 9 and Table 3). q and Θ were estimated from measurements as explained above and substomatal concentrations of CO_2 were estimated from measured CO_2 and H_2O fluxes as explained in Eqs. 1–4. (in Fig. 4 old temperature dependences for J_{max} and $V_{c(max)}$ were used together with previously modelled q, Θ and

Table 5. Modified χ^2 values for measured vs. modelled fluxes with two different temperature dependencies for J_{max} and $V_{c(max)}$ for shoots in Hyytiälä and Värriö. N is the number of degrees of freedom: Number of measurement points – number of variables that have been adjusted to minimize χ^2.

Cuvette	χ^2/N old $V_{c(max)}$ & J_{max}	χ^2/N new $V_{c(max)}$ & J_{max}	N
Värriö 0	2.72	2.56	3369
Värriö 1	19.23	14.83	3283
Värriö 2	4.96	3.54	3235
Hyytiälä 0	3.99	3.53	695
Hyytiälä 5	4.23	3.97	1149

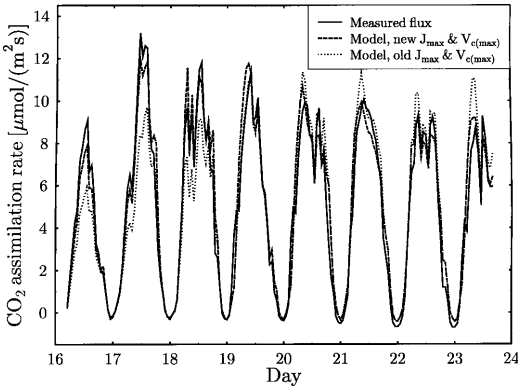

Fig. 8. CO_2 assimilation rate during 16.–23.7 1996 in Värriö cuvette 0 according to measurements and biochemical model with two different temperature dependences for $V_{c(max)}$ and J_{max} (Table 3). Irradiance parameters q and Θ and substomatal concentrations of CO_2 were estimated from measurements. Fluxes are 60 min. averages.

substomatal CO_2, Eqs. 13–14). Results from statistical tests for all shoots using old and new temperature dependences are presented in Table 5. The best agreement with the measured fluxes is obtained with the smallest (modified) χ^2 values. The new sets of parameters for J_{max} and $V_{c(max)}$ showed better response to measurements according to all shoots in Hyytiälä and Värriö. Measured and modelled fluxes with old and new temperature dependences are presented in Fig. 8.

The sensitivity of the resulting flux to changes in different model parameters was studied by decreasing all the parameters in the biochemical model by 10 % and studying the effects in CO_2 assimilation rate. Largest effects were caused by changing J_{max} and $V_{c(max)}$, but according to the usual range of uncertainty of the parameters also K_c, K_o and q (Table 2) may become important in some conditions. Reliable estimations of the irradiance incident to the needles are also important and difficult to make considering the complex structure of the shoot inside the cuvette (see e.g. Oker-Blom et al. 1992).

4 Discussion

The absolute values of flux of CO_2 into unit needle area showed large variation according to measurements. Differences between shoots were clearly seen both in the maximum levels of assimilation and in the responses to environmental variables. The biochemical photosynthesis model produced the same maximum level of assimilation and response to every shoot using temperature, irradiance, relative humidity and ambient concentrations of CO_2 and O_2 as inputs. When measured fluxes were scaled to same level with the biochemical model, the differences became rather small, but some still clearly existed. The discrepancies may be due to difficulties in determining the actual functioning needle area, mean irradiance in needle surfaces, different temperature response etc. These discrepancies are discussed in the following.

Variation in the absolute values of measured flux of CO_2 may be partly due to differences in the actual functioning needle area and, on the other hand, variation in the photosynthetic properties of individual shoots. There were two kinds of shoot settings, flattened and free. Flattened shoots showed smaller fluxes. The area that actually exchanges carbon dioxide is probably smaller than the measured area of flattened twigs, because the needles touch each other. Also the lower surface of the flattened shoot is more effectively isolated from the light. Using lower values for gas exchanging needle surface area the CO_2 flux to unit needle area becomes larger. When all the results were scaled to same level, the model and measurements were in relatively good agreement (correlation coefficient more than 0.90 for four of the five cuvettes)

The temperature dependence of the CO_2 fluxes was examined by choosing those experimental results which were not limited by light or water vapour deficit. According to biochemical photosynthesis model adjusted for southern Finland conditions the CO_2 assimilation rate showed a clear dependence on temperature with a maximum at 16–19 °C (Fig. 5). Cuvette measurements in Hyytiälä agreed relatively well with the model and showed some temperature dependence especially above 18 °C. Agreement with the biochemical model was poor in the Värriö

measurements, which did not show clear dependence on temperature between 5 °C and 18 °C. The level of the maximum daily fluxes did not follow temperature and relative humidity in any Värriö cuvette as closely as the biochemical model indicated (Fig. 5) even according to those shoots which clearly suffered from high temperature and low humidity conditions during some afternoons.

Irradiance was the most important factor controlling the CO_2 flux during the period of time examined. The measured quantum yields (0.025–0.035) are slightly smaller in comparison to the model (Fig. 6). There were no significant differences between flattened and free shoots, or between Hyytiälä and Värriö measurements. Differences between measurements and model are most probably due to shading of the needles. The parameters for the light response of the biochemical photosynthesis model were determined by Wang et al. (1996), who measured the irradiance dependence of carbon dioxide assimilation of a pine shoot in a well controlled environment. The shoot was thinned and carefully illuminated artificially so that shading was minimized. Our cuvette measurements were more approximate, the shoots used were dense and the needles shadowed each other. Irradiance was measured from one place right above the shoot. Probably the measured PAR (photosynthetically active radiation) did not equal the mean irradiance in CO_2 assimilating surfaces (for shading see e.g. Oker-Blom et al. 1992, Leverenz 1996). To examine this, sunny and cloudy mornings were separated from the research material and the quantum yield was calculated for these two cases. During cloudy mornings radiation is more diffuse, i.e. more evenly distributed, and the quantum yield could be higher because PAR measurements better describe the irradiance in needle surfaces. On the other hand, during cloudy or partly cloudy conditions the level of irradiance varies quickly and the response of CO_2 flux to irradiance can be so slow that reliable estimations for CO_2 flux vs. irradiance can not be made from transient values. Quantitative differences were, however, rather difficult to estimate on the basis of these measurements (Fig. 6). More advanced methods for studying the light response of individual shoots are presented in Palva et al. (1997).

Current results for temperature and irradiance dependence of the CO_2 flux agree with the earlier ones. According to Beadle et al. (1985) the photosynthetic rate of Scots pine is strongly dependent on light intensity. During high temperature and low RH periods low conductance may also become a limiting factor. Stomatal conductance depends mainly on water vapour saturation deficit, except during periods of low temperature or light intensity occurring usually at dawn and dusk. Korpilahti (1988) has also found irradiance to be the dominant factor controlling the rate of photosynthesis during the growing season in Hyytiälä. Water deficit usually has only minor influences on photosynthesis in Finnish conditions, but during some dry periods clear effects can be observed. Berry and Björkman (1980) have indicated the importance of adaptation of plants to growing temperature.

Weak temperature dependence of the CO_2 flux in Värriö, due to adaptations to the colder climate, led to re-estimation of the temperature dependence of the main photosynthesis parameters J_{max} and $V_{c(max)}$ from the research material. The parameters were also re-evaluated from Hyytiälä measurements. J_{max} and $V_{c(max)}$ were estimated separately. During the re-evaluation procedure irradiance parameters q and Θ were also estimated from the measurements and conductances of CO_2 were obtained from the exponential curve fitting (Eqs. 1–4). $V_{c(max)}$ showed similar response to temperature according to all shoots in Värriö and Hyytiälä, and was constantly increasing with rising temperature. This result is in relatively good agreement with other estimates (Wang et al. 1996, Wullschleger 1993). Model response was considerably better if J_{max} was allowed to stay high at low temperatures (<18 °C) in Värriö. In Hyytiälä the requirements were not as clear, relatively high J_{max} was also required at high temperatures. The best agreement with measured fluxes was obtained using parameters introduced in Table 3. The new sets of parameters for J_{max} and $V_{c(max)}$ and their performances are also presented in Table 5 and Fig. 8. According to Table 5 best results were obtained with Värriö 0. Värriö 1 suffered from drought effects to some extent and $V_{c(max)}$ was not low enough to force the model to follow measured fluxes during sunny, dry afternoons. It is possible that

there exists better choices for the set of parameters since the fitting is not very sensitive for the shape of the function, but further studies in well controlled environment are required in order to find them out.

The method for processing measurements (Eqs. 1–4) produced also substomatal concentrations of CO_2. The daytime substomatal/ambient concentration was slightly smaller than modelled (Fig. 7). The factor was 0.4–0.8 depending on irradiance conditions etc., while according to the biochemical model it was 0.6–0.9. Anyway, the daytime results do not differ significantly from earlier estimations for conifers by e.g. Brooks et al. (1997). During the night c_i / c_{amb} was almost always above one, whereas the biochemical model did not produce as high nighttime concentrations. This corresponds also to the lower respiration rate in the model. The cloudless nights are not very dark in Värriö during June and July due to the northern location and thus the model easily predicts fluxes that are near zero. Of course, the exponential fitting procedure becomes more difficult during periods of small fluxes, and errors are large when two uncertain results (conductances) are divided by each other.

5 Conclusions

The method described in Eqs. 1–4 for treating cuvette measurements seemed to work well. It produced reasonable conductances and substomatal concentrations of CO_2 with a very simple formulation. The biochemical model agrees relatively well with the cuvette measurements made at Värriö and Hyytiälä during July 1996. The correlation coefficient was over 0.9 for four of the five shoots. Comparisons were mainly performed for relative differences, since uncertainties in determining actually functioning needle areas were large. The best agreement was achieved during rainy days while during dry, bright days the measured fluxes were lower. The effect of lowered afternoon conductances due to low relative humidity on bright, warm days was also observable in assimilation rates in some cuvettes (Värriö 1, and to some extent Värriö 2).

A study of one period of changing weather conditions in Värriö showed that the model followed temperature variations more intensively than the measurements. According to the biochemical photosynthesis model CO_2 assimilation rate showed a clear dependence on temperature with a maximum at 16–19 °C. Cuvette measurements at Värriö did not show a clear dependence on temperature below 18 °C, whereas above 18 °C, mainly according to Hyytiälä measurements, there was an evident negative correlation.

The irradiance response of model and measurements was usually very similar. The quantum yield was slightly smaller according to measurements, but this may be the result of needle shading. There were no significant differences between shoots of different setting, or between Hyytiälä and Värriö measurements. The temperature dependences of J_{max} and $V_{c(max)}$ were estimated from Värriö and Hyytiälä measurements. The results for $V_{c(max)}$ agreed well with earlier estimations. The results for J_{max} indicated relatively high values at low temperatures especially in Värriö. Exact determination of the temperature response of different parameters requires future measurements in a well controlled environment.

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