Parametrization of a biochemical CO_2 exchange model for birch (*Betula pendula* Roth.)

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Gas exchange of one-year-old silver birch (*Betula pendula* Roth.) seedlings of boreal habitat was studied in laboratory conditions. Seedlings were exposed to stepwise changes in CO_2 concentration and irradiance in five constant temperatures ranging from 9 to 33 °C. The Farquhar biochemical model was fitted to the response curves. Values for the photosynthesis parameters J_{max} and $V_{c(max)}$ as well as their temperature dependences were derived from the measurements. Following characteristics of the boreal growth conditions, the response curves were determined also at temperatures below 20 °C. This was, indeed, reflected to photosynthesis parameters, though results showed relatively large variation due to differences among leaves. The gas exchange rates of separate leaves could vary by 40% and also the temperature dependences were slightly different. The slope and curvature of the light response curve were relatively constant above 19 °C and decreased at low temperatures.

Introduction

The gas exchange of leaves is a fundamental process in nature studied in depth for decades. Farquhar *et al.* (1980) introduced a biochemical model for photosynthesis that combines leaf level gas exchange to biochemical processes in chloroplasts. During last years, the model has become widely accepted as a tool for explaining measured leaf CO_2 exchange rates. Certain parameters of the model have to be fitted casewise. These parameters can sometimes be more generally accepted to describe the species if there simultaneously exists awareness of limitations that can be imposed by growth conditions or specific treatments (e.g. Pääkkönen *et al.* 1998, Maurer *et al.* 1997, Ruuska *et al.* 1994, Ovaska *et al.* 1993).

Biochemical model parameters for *Betula pendula* have been estimated and their changes studied by e.g. Rey and Jarvis (1998), Kramer (1995), and Wullschleger (1993) who used measurements of Matyssek *et al.* (1991). These studies cover the changes of parameters due to increasing CO_2 concentration and over growing season. Investigations of the temperature dependence of the parameters are, however, missing. There exists a clear need for determining temperature dependences of the parameters, since there is evidence of differing responses among species (Walcroft *et al.* 1997). Further, these parametrizations are essential for studies on plants acclimating to increasing CO_2 concentration, as along with biochemical changes the temperature dependence of photosynthesis may change as well (e.g. E. Juurola and P. Hari unpubl.).

In this work, we have determined the temperature dependence of $V_{c(max)}$ and J_{max} for mature *Betula pendula* leaves grown in sufficient fertilization and ambient meteorological (ample light) conditions in boreal habitat. In particular, we have examined the behavior of the parameters also below 20 °C, a range often omitted in many current parametrizations made for plants of southern habitat but which is of crucial importance in northern latitudes. The irradiance and CO_2 concentration responses were measured separately in order to obtain all the parameters of the irradiance curve.

Materials and methods

One-year-old nursery-grown silver birch (*Betula pendula* Roth.) seedlings (clones, origin Valkeakoski, Finland) were utilized for gas exchange measurements. The seedlings were planted on 3 June 1998 in eight-liter buckets in a mixture of fertilized peat and sand (2:1, vol:vol). The seedlings were grown outdoors and exposed to ambient variation in light, temperature and air humidity. The gas exchange measurements were performed between 27 July and 5 August 1998 in laboratory conditions. Experimental material consisted of healthy, fully-grown leaves chosen from the top of the seedlings.

To measure gas exchange, an attached leaf was enclosed in a small thermostated cuvette (volume 18 cm³) with a constant airflow (1 dm³ min⁻¹) through it. Dry, CO_2 free air was used as a base gas. The total airflow through the system was regulated with mass flow controllers (5850TR, Brooks Instrument B.V. Netherlands), as well as the injection of CO_2-rich gas (20% CO_2, 80% N_2). Water vapor, generated with a dew point generator, was controlled by a similar mass flow controller. The CO_2 and water vapor concentrations were measured with two IRGAs, infrared gas analyzers, (URAS 3G, Hartmann & Braun AG, Germany). The CO_2 exchange was obtained from the concentration difference between the incoming and outgoing air. For light curves and temperature responses the CO_2 exchange was measured separately with a differential IRGA (URAS 3G, Hartmann & Braun AG, Germany). The light was produced by a daylight lamp (Metallogen HMI, 1200 W/GS, OSRAM GmbH, Germany) and its intensity measured with a PAR sensor (Delta-T Devices, UK). The temperature inside the cuvette was regulated with a control system (computer guided controlling devices Lauda R22 MGW and Lauda RC6 MGW, Königshofen, Germany), and was ascertained by two thermocouples. Ambient room temperature was not controlled, but it stayed relatively stable at about 24 °C. In addition to the throughflow a fan circulated the air inside the cuvette reducing the leaf boundary layer resistance, which was estimated using wetted filter paper as leaf replica and following the procedure by Parkinson (1985). The temperature of the leaf was estimated from the energy balance as in Hall *et al.* (1993). The leaf area was determined graphically and the gas exchange results were expressed on total leaf area (one-sided) basis.

For the response curves three leaf replicas were used, each from a different seedling. Prior to the measurements the leaf was acclimated to saturating irradiance (1500 µmol m⁻² s⁻¹) and measurement temperature for half an hour. The CO_2 concentration in the cuvette was gradually decreased from 360 ppm to about 20 ppm through five steps, increased back to 360 ppm and then the leaf was allowed to acclimate for at least five minutes. After that the concentration was increased to about 1000 ppm through five steps.

Each step took 180–240 s of stabilizing time

and 180 s of recording time. Transpiration and conductance increased steeply at low CO_2 concentrations indicating stomatal opening. The conductance usually decreased near to the original level during measurements in high concentrations. After the measurement of the assimilation vs. CO_2 curve the CO_2 concentration was about 1000 ppm. The irradiance response of the CO_2 assimilation rate was measured in these conditions by decreasing the PAR level from 1800 µmol m⁻² s⁻¹down to 2–5 µmol m⁻² s⁻¹ through 12 steps. The total time for acclimation to saturating irradiance before measuring the irradiance response curve was over 1.5 hours. These two response curves were measured at five (leaf) temperatures (9, 14, 19, 25 and 33 °C). Finally, the temperature response of dark (non-photorespiratory) respiration rate was measured by setting the irradiance to 2–5 µmol m⁻² s⁻¹, CO_2 level to 360 ppm and changing the temperature from 9 to 33 °C through ten steps each lasting for about half an hour. The CO_2 assimilation rate was measured using the same method and setting the irradiance level to 900 µmol m⁻² s⁻¹ and CO_2 to 360 ppm.

The data were analyzed with Matlab⸴ 5.2. The packages used in fitting procedures utilized the Nelder-Mead simplex search algorithm (Nelder and Mead 1965) for minimizing functions of several variables and the golden section search and parabolic interpolation algorithm for minimizing functions of one variable. The factor to be minimized was the square of the norm (largest singular value) of the error matrix. The error matrix (or vector in this case, thus the factor corresponds to error-weighed RMS-value) was calculated as modelled values minus measured values and the result was divided by the error of the measurement. For example, for assimilation rate calculations the error of the measurement was assumed to equal 5% of measured flux value + constant (0.5 µmol m⁻² s⁻¹)

Biochemical model

The model of Farquhar *et al.* (1980) was utilized in a form presented by Harley and Baldocchi (1995) and Lloyd *et al.* (1995). According to the model the CO_2 carboxylation rate is limited either by RuBP (ribulose 1,5-bisphosphate) regenera-

tion or Rubisco (ribulose 1,5-bisphosphate carboxylase/oxygenase) activity. A third option would be rate limitation by nutrient availability, but it can be ignored here since the seedlings were sufficiently fertilized. The net rate of CO_2 exchange equals the rate of carboxylation minus photorespiration minus dark respiration. It can be written as

$$A_j = \min(A_j, A_c) \qquad (1)$$

where A_j is the RuBP regeneration limited rate of the net CO_2 exchange and can be written as (Lloyd *et al.* 1995)

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

and A_c is the net Rubisco-limited rate (Lloyd *et al.* 1995):

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

In Eqs. 2 and 3 $V_{c(max)}$ is the maximum rate of carboxylation with non-limiting RuBP and CO_2 and with full activation of Rubisco, J is the potential electron transport rate (related to the potential rate of carboxylation as stated by von Caemmerer and Farquhar 1981), R_d is the rate of non-photorespiratory respiration, k_c is the Michaelis-Menten constant for CO_2, k_o is the Michaelis-Menten constant for O_2, Γ_* is the CO_2 compensation point in the absence of non-photorespiratory respiration, o is the oxygen concentration in chloroplasts and c_i is the carbon dioxide concentration in chloroplasts. c_i was assumed to equal the CO_2 concentration in the intercellular airspaces, a variable which can be quantified by simultaneous transpiration and CO_2 exchange measurements (von Caemmerer and Farquhar 1981).

According to Lloyd *et al.* (1995) (*see also* Farquhar and Wong 1984) the dependence of J on irradiation (I_0) can be written as

$$J = \frac{qI_0 + J_{max} - \sqrt{(qI_0 + J_{max})^2 - 4\Theta qI_0 J_{max}}}{2\Theta} \quad (4)$$

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

Θ and q were estimated from current measurements.

The Arrhenius type of relationship presented by e.g. Harley and Baldocchi (1995) was used for temperature dependences of certain parameters:

$$f_T = f_{298} \exp\left[\frac{E_f(T - 298.15)}{298.15RT}\right] \qquad (5)$$

where f denotes the parameter, i.e. $V_{c(max)}$, R_d, k_c or k_o, and E_f is the activation energy of the specific parameter. The following equation (*see* list of symbols in Appendix) was used for J_{max} (Lloyd *et al.* 1995, Farquhar *et al.* 1980):

$$J_{max} = \frac{B \exp\left[\frac{E_j(T/298.15 - 1)}{RT}\right]}{1 + \exp\left[\frac{S_j T - H_j}{RT}\right]}. \qquad (6)$$

Temperature dependences of J_{max}, $V_{c(max)}$ and R_d were estimated from current measurements. Temperature dependence of Γ_* in Eqs. 2 and 3 was adopted from Brooks and Farquhar (1985).

Model parametrization

The model was parametrized using measurements of carbon assimilation responses for intercellular CO_2 and irradiance and measurements of dark respiration rate.

Non-photorespiratory respiration in light and dark

Non-photorespiratory respiration rate was determined from measurements of carbon production rate in total darkness in ten different temperatures. The conductance decreased slightly in high temperatures, but the production rate was correlated with temperature more strongly than with the conductance. Non-photorespiratory respiration rate in dark from zero irradiance points in *A/I* curves also agreed with these measurements.

Non-photorespiratory respiration rate in light (R_d) was determined from three to five lowest

points of A/c_i curves by fitting a straight line through measurement points. The conductance increased towards lower CO_2 concentrations in several cases. The measurement cycle appeared to be too fast to attain equilibrium between assimilation rate and increasing conductance at each step leading to high exchange rates at low concentrations. R_d was therefore determined from selected measurements where conductance did not change more than 20% during the first part of the cycle and for the rest of the curves the two lowest points were abandoned. Non-photorespiratory respiration in dark appeared to be related to R_d by a factor of 1.41. The transition to daylight values was assumed to occur sharply at 10 µmol m^{-2} s^{-1} (according to e.g. Lloyd *et al.* (1995) the non-photorespiratory respiration in dark and R_d are equal below that limit). Values for R_d are also in accordance with the relation suggested by Collatz *et al.* (1991): $R_d = 0.015V_{c(max)}$. According to our measurements $R_d = 0.017V_{c(max)}$ at 25 °C. The temperature response of R_d was assumed to be similar to that of the non-photorespiratory respiration in dark. Values for the parameters in the temperature dependence function for R_d (Eq. 5) are presented in Table 1.

J_{max} and other parameters related to the irradiance curve

Parameters in Eq. 2 were fitted using measured *A/I*-curves. Since there are too many free parameters to reliably fit simultaneously (J_{max}, q and Θ) the problem was divided into parts. q, the initial slope, was solved first keeping Θ constant and weighing measurements near the irradiance compensation point. At 19 °C and above that q was very stable (near 0.16) but at the two lowest temperatures (9 °C and 14 °C) q was clearly lower (*see* points just above zero in Fig. 1). In order to attain a good fit, q had to be expressed as a function of temperature (*see* Table 1).

A similar conclusion was drawn for the curvature factor Θ. Θ was solved from the whole *A/I* research material using the estimation above for q and freely varying J_{max}. At 19 °C and above that Θ was quite constant showing only small increase (0.90→0.92) but at the two lowest temperatures

Fig. 1. Irradiance response of the CO_2 exchange rate at 5 constant temperatures and ambient CO_2 concentration of 1000 µmol mol⁻¹. Lines refer to modelled exchange rates. The measured differences in gas exchange rates among the three leaf replicas are shown as bars. The length of the bar corresponds to the lowest and highest CO_2 assimilation rate observed at each temperature and irradiance. Circles refer to the mean exchange rates.
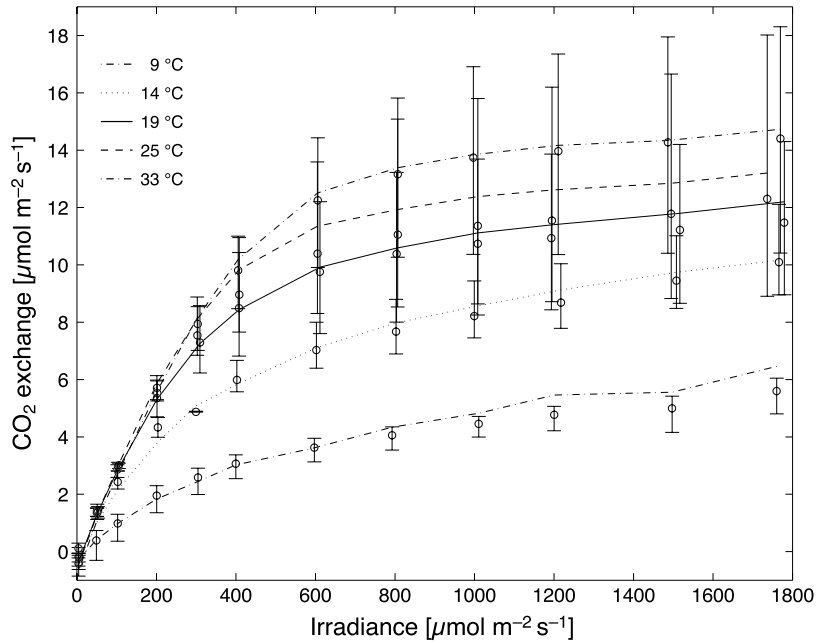
(9 °C and 14 °C) the A/I curve was smoother and Θ had to be strongly modified. The temperature dependence of Θ was smoothed over the measurement range for best possible fit to data points resulting in the equation presented in Table 1. Values of q were also verified using new estimation for Θ. For q and Θ there were no large differences among leaves.

After q and Θ were fixed, J_{max} was solved at each temperature for every leaf separately and for the three leaves together using Eq. 2. To confirm the result, J_{max} was also evaluated from the four last points of the A/c_i-curves where c_i was above 500 µmol mol⁻¹. The results were very similar for both sets of curves. The temperature dependence of J_{max} was adopted from Eq. 6 and parameters E_j, S_j, H_j and B (Table 1, Appendix) were determined from results for J_{max} at different temperatures (*see* resulting fit in Fig. 2). J_{max} showed quite large variability among leaves. The parameter B is related to the frequently used $J_{max,298K}$ (*see* Appendix). The corre-

Table 1. Values for biochemical model parameters in Eqs. 4–6 fitted from measurements with *Betula pendula* Roth. leaves. Error estimate corresponds to variation among parameters fitted for each leaf separately. T is temperature in °K. *: R_d must be multiplied by 1.41 in totally dark conditions (< 10 µmol m⁻² s⁻¹). Fit for temperature dependence of J_{max} should be used only below 307 °K and for Θ and q only above 280 °K.

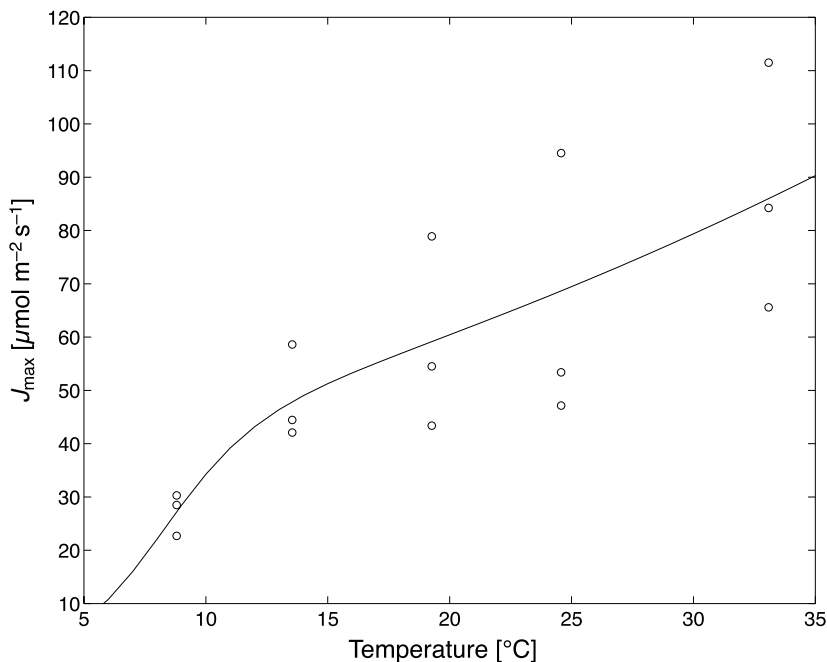| Parameter	Value	Error
E_j	370 000 J mol⁻¹	20%
S_j	1245.5 J mol⁻¹ K⁻¹	18%
H_j	350 000 J mol⁻¹	19%
B	381 700 µmol m⁻² s⁻¹	40%
$E_{Vc(max)}$	64 500 J mol⁻¹	12%
$V_{c(max),298}$	26.7 µmol m⁻² s⁻¹	29%
E_{Rd}	26 000 J mol⁻¹	9%
$R_{d,298}$	*0.44 µmol m⁻² s⁻¹	14%
q	$0.162 - \exp(-0.209T + 56.5)$	8% (298 °K)
Θ	$0.930 - \exp(-0.014628T^2 + 8.2336T - 1158.8)$	3% (298 °K)

Fig. 2. Temperature dependence of J_{max}. Circles are values of J_{max} deduced from measured A/I curves at different temperatures and solid line the fit.

sponding values for $J_{max,298K}$ were in the range (55.4–93.4) µmol m^{-2} s^{-1} depending on the individual leaf.

The resulting fit for Eq. 2 using new estimations for parameters q, Θ and J_{max} and R_d was used to determine the rate of CO_2 exchange at the five measurement temperatures (Fig. 1). The model performed best at high temperature and moderate irradiance conditions, but also in other conditions the curves stayed inside the range determined by the leaf to leaf variation.

Maximum rate of carboxylation ($V_{c(max)}$)

$V_{c(max)}$ was estimated from A/c_i curves using R_d independently obtained from the same curves. Eq. 3 was fitted to the lower part of the curve and $V_{c(max)}$ was solved (assimilation rate appeared to be limited by J_{max} at concentrations above 400–500 µmol mol^{-1}). $V_{c(max)}$ was fitted for leaves separately and for the whole research material, one $V_{c(max)}$ to each temperature Θ (Figs 3 and 4).

The resulting temperature dependences of $V_{c(max)}$ for different leaves agreed quite well with each other. The functional form of Eq. 5 was easily adopted (Fig. 5). Some uncertainty en-

tered to results through quite large variability in leaf gas exchange levels (max. 40% differences between leaves, *see also* variation in $V_{c(max)}$ in Fig. 5) suggesting that the requirement of a large number of replicas would have been justified. However, as we wanted to determine the environmental responses in the end of the growth season, but before the offset of photosynthesis, while the seedlings were in the same growth phase, the measurements had to be completed in a short time. Values for parameters in Eq. 5 for $V_{c(max)}$ are presented in Table 1.

Comparison to measurements at ambient CO_2

The parametrization was tested against steady state temperature responses at ambient CO_2 measured using the same leaf material. Irradiance was set to 900 µmol m^{-2} s^{-1} and the temperature was increased from 9 to 33 °C through 10 steps each lasting for half an hour. The model showed a very similar temperature response in comparison to the measurements (Fig. 6). According to the model, the temperature maximum is near 25 °C because of the decreasing conductance at high

Fig. 3. Dependence of the net CO_2 exchange rate on the intercellular CO_2 concentration c_i at saturating irradiance (1500 µmol m^{-2} s^{-1}). Circles are measurement points for the three leaves at 25 °C and dashed line the fitted model curve.

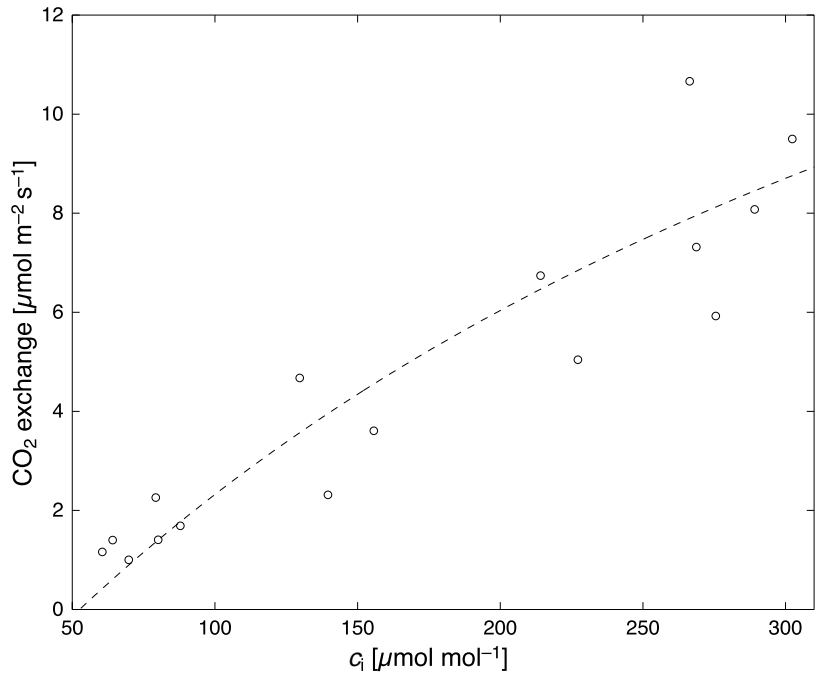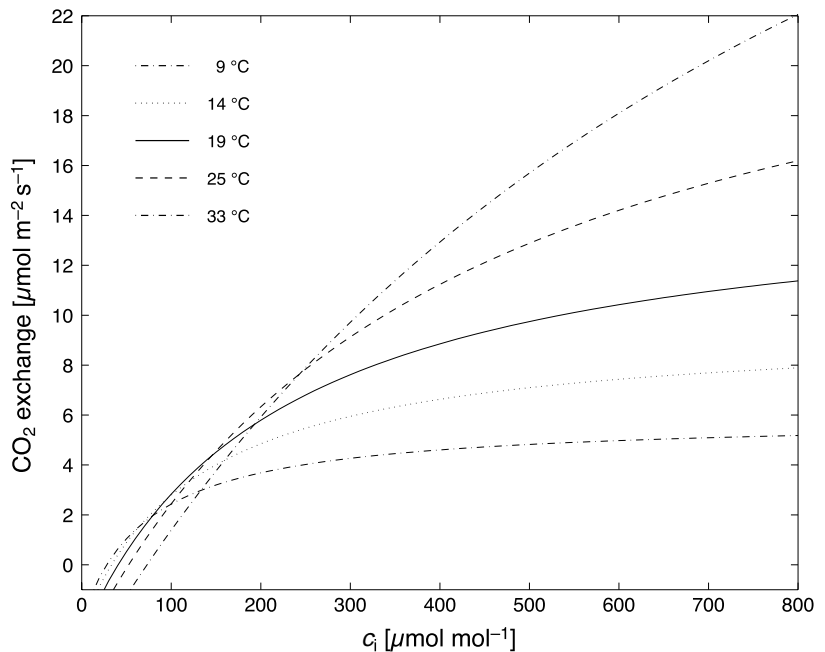**Fig. 4**. Dependence of the net CO_2 exchange rate on the intercellular CO_2 concentration c_i at saturating irradiance (1500 µmol m^{-2} s^{-1}). Lines refer to the modelling results at different temperatures.

temperatures. Under conditions allowing the conductance to be constant it would be slightly higher. The CO_2 exchange level was relatively high according to the model, but the leaves also differ from each other by over 30%, suggesting large variability in the material.
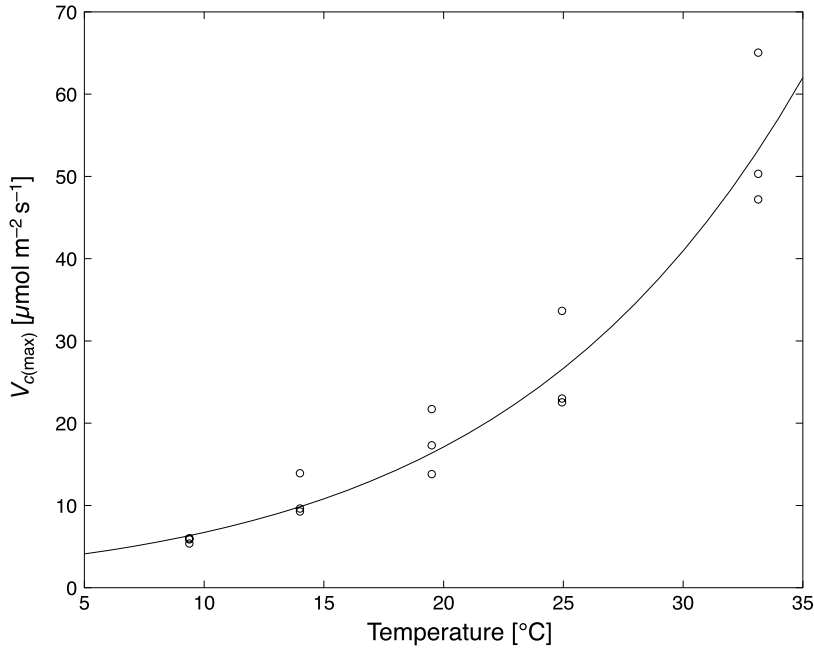
Fig. 5. Temperature dependence of $V_{c(max)}$. Circles are values of $V_{c(max)}$ deduced from measured A/c_i curves at different temperatures and solid line the fit.
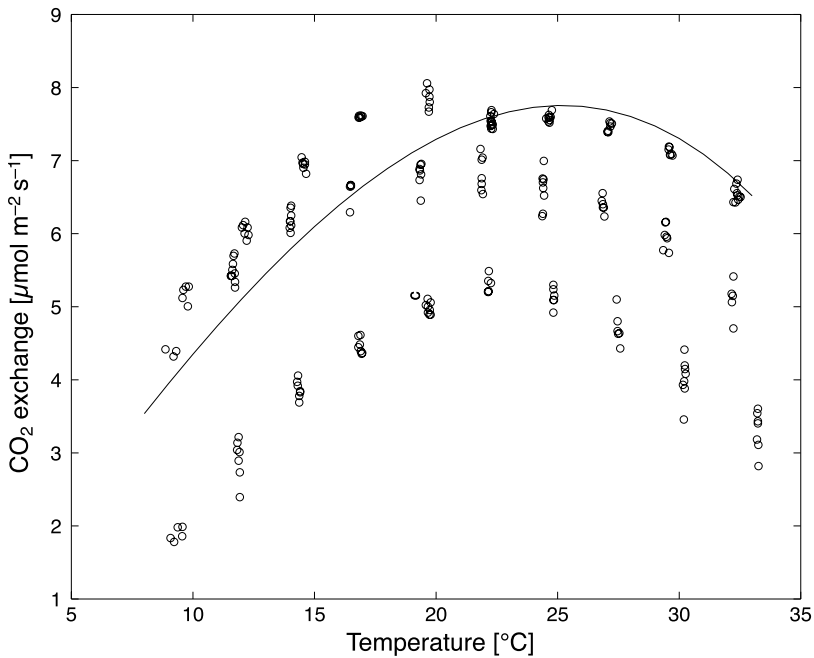

Fig. 6. Temperature dependence of the CO_2 exchange at ambient CO_2 concentration of 360 µmol mol^{-1} and saturating irradiance. Solid line refers to model and symbols to measurements with three leaves.

Discussion and conclusions

J_{max} showed quite large variability among leaves (over 40%, *see* Fig. 2). The mean values for J_{max} are somewhat lower than estimates for *Betula pendula* by Rey and Jarvis (1998) or the value

used by Wullschleger (1993) but on the other hand e.g. Maurer *et al.* (1997), Pääkkönen *et al.* (1998) and Ovaska *et al.* (1993) measured similar relatively low levels of gas exchange using young *Betula pendula* clones. The fitted function for the temperature dependence of J_{max} was

found to be continuously increasing (Fig. 2), while others have often found a maximum in the J_{max}/T-curve (e.g. Walcroft *et al.* 1997). Here the maximum can not be located, possibly due to sparsely located measurement points in the region. The region of validity for the fit is therefore strictly limited to temperatures below 34 °C. A good fit of Eq. 6 with various free parameters requires several measurement points. More points would have been needed in the present work especially in the temperature range between 20 °C and 35 °C.

Our model parameter q is the quantum yield of electrons/quanta dependent on the leaf reflectance, absorptance and the spectral imbalance for use of light (Lloyd *et al*, 1995, Evans, 1987). It was found to be quite constant at high temperatures and clearly lowered at 9 and 14 °C. According to the literature, the apparent quantum yield (mol CO_2/mol quanta) usually decreases with rising temperature and increases with increasing CO_2 concentration (e.g. Cannell and Thornley 1998). At saturating CO_2 concentrations, the apparent quantum yield is almost constant over a wide range of temperatures (Cannell and Thornley 1998). Our modelled apparent quantum yield (at typical c_i of 250 µmol mol⁻¹) increased up to 21 °C due to the observed low temperature effect in q, then turned to a slight decrease due to an increase in respiration and competitive inhibition of oxygen causing a decrease in the carboxylation rate of RuBP (included in the basic model structure). Studies at c_i of 700 µmol mol⁻¹ showed a higher apparent quantum yield which only decreased in temperatures above 25 °C. Our estimations generally agree with earlier results, but the reason for low values at 9 and 14 °C remains to be solved. For example, Leverenz and Öquist (1987) found low quantum yields in cold-tolerant pine (below 5 °C) due to low temperature stress suggesting the possibility for sensitive response to environmental stress factors also in our measurements.

Our estimations for the curvature Θ showed a decrease at 9 and 14 °C and a quite constant level at high temperatures (Θ = 0.9–0.92). Θ is often considered to be an entirely empirical factor determined by curve fitting (e.g. Cannell and Thornley 1998) but it has also been found to depend on the amount of chlorophyll, the gradient in light absorption and photosynthetic capacity in leaves and maybe also the partial pressure of CO_2 (Leverenz 1988, Ogren and Evans 1993, Evans *et al.* 1993). A typical Θ for a C3 plant is near 0.97 (e.g. Terashima and Saeki 1985) and it should be relatively independent of temperature for an un-stressed leaf between 5 °C and 32 °C (Leverenz 1988). However, for a light-stressed leaf Θ can be lowered due to photoinhibition (Leverenz *et al.* 1990), and according to Terashima *et al.* (1991) simultaneous low temperature and light treatment can increase stress and cause uncoupling of the thylakoids in chilling-sensitive plants. The low Θ values observed in this study at 9 and 14 °C can thus be due to stress caused by light and low temperature. The same applies for q.

The $V_{c(max)}$ results (Fig. 5) agree with J_{max} levels ($J_{max}/V_{c(max)}$=2.6 at 25 °C) and are slightly lower than corresponding estimates in the literature. At 22 °C our value for $V_{c(max)}$ is 20 µmol m⁻² s⁻¹ while Ruuska *et al.* (1994) gave an estimate of about 26 µmol m⁻² s⁻¹ for *Betula pendula*, Rey and Jarvis (1998) 22 µmol m⁻² s⁻¹ at 21 °C and Wullschleger (1993) 34 µmol m⁻² s⁻¹ at 20 °C. Our leaf to leaf variation exceeds 30% which indicates variation of at least ± 3 µmol m⁻² s⁻¹ in the $V_{c(max)}$ value at 22 °C. $V_{c(max)}$ was constantly increasing when temperature was increased. The results indicated only minor corrections to parameters of the classical response function (e.g. Lloyd *et al.* 1995).

Values obtained for R_d (Table 1) are also typical for a deciduous tree (e.g. Harley and Baldocchi 1995). According to our parametrization the CO_2 compensation concentration in the presence of dark respiration (G) for *Betula pendula* was 42.5 µmol mol⁻¹ at 20 °C. For comparison, according to measurements by Ruuska *et al.* (1994) it was near 30 µmol mol⁻¹ at 22 °C and 45 µmol mol⁻¹ by Pettersson and McDonald (1992) at 20 °C. G of 30 µmol mol⁻¹ seems quite low for 22 °C, since Γ_* , compensation point in the absence of non-photorespiratory respiration, is already 39 µmol mol⁻¹ at 22 °C (Brooks and Farquhar 1985) suggesting that Γ should be even higher. Lloyd *et al.* (1995) assumed that R_d experiences variations according to irradiance also at high light intensities, but in this context it is impossible to verify.

Instead, we have utilized the usual assumption of sharp change to dark respiration at irradiances below 10 µmol m^{-2} s^{-1} (e.g. Lloyd *et al.* 1995).

The verification of parametrization against steady-state temperature response at ambient CO_2 of 360 µmol mol^{-1} showed good results. The model predicted the temperature maximum correctly when compared to the independently measured response curve (Fig. 6). The three leaves showed extensive variation in the level of gas exchange. The variation was not largely due to changes in conductance (or changes in conductance were alike), because the modelled curve was similar for every leaf.

As a conclusion, the model represented the responses of single birch leaves to changing temperature, irradiance and CO_2 concentration with adequate precision. This parametrization for photosynthesis of birch leaves can be used as a submodel in models describing boreal zone ecosystem functioning or utilized for smaller scale studies on leaf level photosynthesis. However, care must be taken when applying responses of leaves in seedlings to leaves in canopies and old trees (*see* e.g. Yoder *et al* 1994, Kelly *et al.* 1995).

The current parametrization for birch will be utilized in the near future for construction of a three-dimensional transport model for CO_2 and H_2O molecules inside a leaf with explicitly described mesophyll cells and air spaces (*see* Aalto *et al.* 1999). Modelling results will be compared to measurements of localized CO_2 uptake in mesophyll cells. The present birch parametrization will describe the biochemical sink for CO_2 in chloroplasts. Further on, the problems of connecting a leaf-level area-based description of photosynthesis and an actual 3D description of sinks in a transport frame will be considered and the consequences to the photosynthesis model parameters clarified.

References

Aalto T., Vesala T., Mattila T., Simbierowicz P. & Hari P. 1999. A three-dimensional stomatal CO_2 exchange model including gaseous phase and leaf mesophyll separated by irregular interface. *J. Theor. Biol.* 196(1): 115–128.

Brooks A. & Farquhar G.D. 1985. Effect of temperature on the CO_2/O_2 specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. *Planta* 165: 397–406.

Cannell M.G.R. & Thornley J.H.M. 1998. Temperature and CO_2 responses of leaf and canopy photosynthesis: a clarification using the non-rectangular hyperbola model of photosynthesis. *Ann. Bot.* 82: 883–892.

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. *Agr. For. Met.* 54: 107–136.

Evans J.R. 1987. The dependence of quantum yield on wavelength and growth irradiance. *Aust. J. Plant Phys.* 14: 69–79.

Evans J.R., Jakobsen I. & Ogren E. 1993. Photosynthetic light-response curves: 2. Gradients of light absorption and photosynthetic capacity. *Planta* 189(2): 191–200.

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.

Farquhar G.D. & Wong S.C. 1984. An empirical model of stomatal conductance. *Aust. J. Plant Phys* 11: 191–210.

Hall D.O., Scurlock J.M.O., Bolhàr-Nordenkampf H.R., Leegood R.C. & Long S.P. 1993. *Photosynthesis in a Changing Environment. A Field and Laboratory Manual.* Chapman & Hall, London, UK

Harley P.C. & Baldocchi D.D. 1995. Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. I. Leaf model parametrization. *Plant Cell Env.* 8: 1146–1156.

Kramer K. 1995. Modelling comparison to evaluate the importance of phenology for the effects of climate change on growth of temperate-zone deciduous trees. *Climate Res.* 5: 119–130.

Kelly J.M., Samuelson L., Edwards G., Hanson P., Kelting D., Mays A. & Wullschleger S. 1995. Are seedlings resonable surrogates for leaves? An analysis of ozone impacts on *Quercus rubra*. *Water Air and Soil Poll.* 85: 1317–1324.

Leverenz J.W. & Öquist G. 1987. Quantum yields of photosynthesis at temperatures between –2 °C and 35 °C in a cold-tolerant C_3 plant *Pinus sylvestris* during the course of one year. *Plant Cell Env.* 10: 287–295.

Leverenz J. 1988. The effects of illumination sequence, CO_2 concentration, temperature and acclimation on the convexity of the photosynthetic light response

curve. *Phys. Plant.* 74: 566–574.

Leverenz J.W., Falk S., Pilström C.M. & Samuelsson G. 1990. The effects of photoinhibition on the photosynthetic light-response curve of green plant cells (*Chlamydomonas reinhardtii*). *Planta* 182(2): 161–168.

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

Matyssek R., Gunthardt-Goerg M., Keller T. & Scheidegger C. 1991. Impairment of gas exchange and structure in birch leaves (*Betula pendula*) caused by low ozone concentrations. *Trees* 5: 5–13.

Maurer S., Matyssek R., Gunthardt-Goerg M., Landolt W. & Einig W. 1997. Nutrition and the ozone sensivity of birch (*Betula pendula*) I. Responses at the leaf level. *Trees* 12: 1–10.

Nelder, J. A. & R. Mead 1965. A Simplex Method for Function Minimization. *Computer Journal* 7: 308–313.

Ogren E. & Evans J.R. 1993. Photosynthetic light-response curves: I. The influence of carbon dioxide partial pressure and leaf inversion. *Planta* 189(2): 182–190.

Ovaska J., Ruuska S., Rintamäki E. & Vapaavuori E. 1993. Combined effects of partial defoliation and nutrient availability on cloned *Betula pendula* saplings II. Changes in net photosynthesis and related biochemical properties. *J. Exp. Bot.* 44(265): 1395–1402.

Parkinson K.J. 1985. A simple method for determining the boundary layer resistance in leaf cuvettes. *Plant Cell Env.* 8: 223–226.

Pettersson R. & McDonald A. 1992. Effects of elevated carbon dioxide concentration on photosynthesis and growth of small birch plants (*Betula pendula* Roth.) at optimal nutrition. *Plant Cell Env* 15: 911–919.

Pääkkönen E., Vahala J., Pohjola M., Holopainen T & Kärenlampi L. 1998. Physiological, stomatal and ultrastructural ozone responses in birch (*Betula pendula* Roth.) are modified by water stress. *Plant Cell Env.* 21: 671–684.

Rey A. & Jarvis P.G. 1998. Long-term photosynthetic acclimation to increased atmospheric CO$_2$ concentration in young birch (*Betula pendula*) trees. *Tree Phys* 18: 441–450.

Ruuska S., Vapaavuori E. & Laisk A. 1994. Reactions of birch leaves to changes in light during early ontogeny: comparison between *in vivo* and *in vitro* techniques to measure carbon uptake. *J. Exp. Bot.* 45(272): 343–353.

Terashima I. & Saeki T. 1985. A new model for leaf photosynthesis incorporating the gradients of light environment and of photosynthetic properties of chloroplasts within a leaf. *Ann. Bot.* 56: 489–499.

Terashima I., Sonoike K., Kawazu T. & Katoh S. 1991. Exposure of leaves of *Cucumis Sativus* L. to low temperatures in the light causes uncoupling of thylakoids II. Non-destructive measurements with intact leaves. *Plant Phys.* 32(8): 1275–1283.

von Caemmerer S. & Farquhar G.D. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153: 376–387.

Walcroft A., Whitehead D., Silvester W. & Kelliher F. 1997. The response of photosynthetic model parameters to temperature and nitrogen concentration in *Pinus Radiata* D.Don. *Plant Cell Env.* 20: 1338–1348.

Wullschleger S. 1993. Biochemical limitations to carbon assimilation in C3 plants — A retrospective analysis of the *A/c$_i$* curves from 109 species. *J. Exp. Bot.* 44(262): 907–920.

Yoder B.J., Ryan M.G., Waring R.H., Schoettle A.W. & Kaufmann M.R. 1994. Evidence of reduced photosynthetic rates in old trees. *For. Sci.* 40(3): 513–527.

Appendix. Definitions and literature values for parameters in biochemical model.

Symbol	Definition and units	Value
A	CO_2 assimilation rate (µmol m⁻² s⁻¹)	
A_c	Rubisco-limited rate of assimilation (µmol m⁻² s⁻¹)	
A_j	RuBP-regeneration limited rate of assimilation (µmol m⁻² s⁻¹)	
B	Constant $\left\{ = J_{max,298} \times \left[1 + \exp\left(\dfrac{298 S_j - H_j}{298 R} \right) \right] \right\}$ (µmol m⁻² s⁻¹)	
c_i	CO_2 concentration in intercellular spaces (µmol mol⁻¹)	
E_f	Activation energy (J mol⁻¹)	
E_j	Activation energy for RuBP-regeneration limited assimilation rate (J mol⁻¹)	
E_{kc}	Activation energy for k_c (J mol⁻¹)	80 500[a]
E_{ko}	Activation energy for k_o (J mol⁻¹)	14 500[a]
E_{Rd}	Activation energy for respiration (J mol⁻¹)	
$E_{Vc(max)}$	Activation energy for Rubisco-limited assimilation rate (J mol⁻¹)	
H_j	Deactivation energy for RuBP-regeneration limited assimilation rate (J mol⁻¹)	
I_0	Incident irradiance (µmol m⁻² s⁻¹)	
J	Potential rate of electron transport (µmol m⁻² s⁻¹)	
J_{max}	Maximum rate of electron transport (µmol m⁻² s⁻¹)	
$k_{c,298}$	Michaelis-Menten constant for CO_2 (µmol mol⁻¹)	275[a]
$k_{o,298}$	Michaelis-Menten constant for O_2 (µmol mol⁻¹)	420 000[a]
o	O_2 concentration in intercellular spaces (µmol mol⁻¹)	210 000
q	Effectivity factor for the use of light (mol e⁻/mol quanta)	
R	Gas constant (J mol⁻¹ K⁻¹)	8.314
R_d	Non-photorespiratory respiration (µmol m⁻² s⁻¹)	
S_j	Entropy of the denaturation equilibrium for RuBP-regeneration limited assimilation rate (J mol⁻¹ K⁻¹)	
T	Temperature (K)	
$V_{c(max)}$	Maximum rate of carboxylation (µmol m⁻² s⁻¹)	
$\Gamma_{*,298}$	CO_2 compensation point in the absence of non-photorespiratory respiration (µmol mol⁻¹)	31[b]
Θ	Convexity factor of the light response curve	

[a] Harley and Baldocchi (1995) and [b] Brooks and Farquhar (1985)